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*Cover photo:* Fence covered by ballooning *Collinsia ksenia* (Crosby & Bishop) near McBride, British Columbia. Photo by Doug Wilson.

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# LIFE HISTORIES OF FOUR SPECIES OF SCORPION IN THREE FAMILIES (BUTHIDAE, DIPLOCENTRIDAE, VAEJOVIDAE) FROM ARIZONA AND NEW MEXICO

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**ABSTRACT.** Although scorpions are common and potentially ecologically important members of arid ecosystems throughout the world, basic life history information is lacking for most species. In the current study I examined reproductive investment patterns in four species of scorpion (*Centruroides exilicauda, Vaejovis spinigerus, Diplocentrus peloncillensis,* and *Pseudouroctonus apacheanus*) from southeastern Arizona and southwestern New Mexico during 1996–1998. *Vaejovis spinigerus* invested more in reproduction, in both absolute (total litter mass, TLM) and relative (TLM divided by female mass) terms, than did the other species, and produced the largest litters. Offspring of *D. peloncillensis* were the largest, weighing over twice as much as the next largest juveniles. Female size was uncorrelated with offspring size in any species, but positive correlations were found between female size and both litter size and total litter mass for *C. exilicauda* (marginally significant) and *V. spinigerus* (after removal of an outlier). Greater reproductive investment, measured as TLM, was used to make more offspring (in all species but *P. apacheanus*) but not larger offspring. A marginally significant trade-off between offspring size and number was found in *V. spinigerus*; there was no size-number trade-off in the other three species. Overall, then, my results suggest that (1) larger females do not produce larger offspring, (2) larger females may produce more offspring and invest more into a reproductive bout, and (3) the allocation strategy of these species appears to be to invest reproductive resources into production of as many offspring as possible of a relatively fixed size.

**Keywords:** reproductive investment, scorpions, offspring size, litter size, trade-offs

One of the primary goals of life history studies is to understand how females allocate energy into reproduction, both within a single reproductive event and across their lifespan (Roff 1992, 2002; Stearns 1992). A female's allocation strategy for a single clutch may be thought of in terms of two "decisions." First, she must choose how much of her available resources to devote to reproduction (i.e., reproductive effort or investment). Second, she must decide how to allocate that resource fraction into offspring (i.e., per-offspring investment; Bernardo 1996). The latter decision is generally modeled as a trade-off between making a few large or many small offspring, and a number of studies in various taxa have demonstrated such a trade-off (reviews in Roff 1992; Stearns 1992). Reproductive effort and per-offspring investment have usually been assumed to evolve independently (e.g., Smith & Fretwell 1974; Roff 1992, 2002; Stearns 1992), although recent theoretical and empirical evidence suggest they are likely linked evolutionarily (Winkler & Wallin 1987; Caley et al. 2001). Thus, reproductive effort, litter size, and offspring size potentially covary at the phenotypic level. Furthermore, these three traits often vary with female size, which itself is often under strong selective pressure (Roff 1992, 2002; Stearns 1992).

Based on the above, reproductive allocation patterns are best understood when multiple traits are measured for each of a number of females within a species. For scorpions, such studies are unfortunately rare (Francke 1981; Bradley 1984; Benton 1991a, b; Formanowicz & Shaffer 1993; Brown & Formanowicz 1995, 1996; Lourenço et al. 1996). These studies indicate that, with a few exceptions, female size is unrelated to offspring size. However, larger females generally produce larger litters and have a greater reproductive investment, measured as total litter mass, than smaller females, although these trends do not hold for all species or even all populations of a single species (Brown 2001). Females with greater investment most often simply increase the number of offspring produced, although in

Table 1.—Descriptive statistics (mean ± SE) for life history traits in *Centruroides exilicauda*, *Vaejovis spinigerus*, *Diplocentrus peloncillensis*, and *Pseudouroctonus apacheanus* from Arizona and New Mexico. CL = carapace length. CV = coefficient of variation. A dash indicates that a variable was unmeasured. Masses are in mg. Carapace lengths are in mm. Instar 1 duration is in days.

| | Female mass | Female CL | Mean offspring mass | Mean offspring CL | Litter size |
|---|---|---|---|---|---|
| 1996 *C. exilicauda* | 425.2 ± 16.1 | 4.75 ± 0.06 | 9.4 ± 0.3 | 1.57 ± 0.02 | 16.4 ± 1.4 |
| 1997 *C. exilicauda* | 373.3 ± 9.7 | 4.79 ± 0.03 | 10.3 ± 0.4 | — | 12.7 ± 1.1 |
| 1996 *V. spinigerus* | 882.8 ± 96.1 | 6.41 ± 0.21 | 9.8 ± 0.5 | — | 49.2 ± 4.6 |
| All *V. spinigerus* | 828.4 ± 64.8 | 6.39 ± 0.14 | 9.4 ± 0.4 | — | 48.4 ± 4.0 |
| *D. peloncillensis* | 897.2 ± 57.9 | 5.42 ± 0.09 | 23.8 ± 1.5 | — | 13.0 ± 1.1 |
| *P. apacheanus* | 153.4 ± 17.9 | 3.66 ± 0.13 | 1.6 ± 0.2 | — | 27.8 ± 4.2 |

some cases (Formanowicz & Shaffer 1993; Brown & Formanowicz 1995) larger offspring are also made. Finally, most species do not exhibit an offspring size-number trade-off, and for those that do the strength and direction of the trade-off can vary among populations or years (Brown 2001).

The life history of scorpions is virtually unique among terrestrial arthropods (Polis & Sissom 1990). They are often long-lived and relatively large at maturity. Females give birth to live young, potentially producing multiple litters over a number of years, and provide parental care through at least the first molt. Scorpions are also potentially ecologically important predators in many arid and tropical ecosystems (Polis 2001), and knowledge of their life histories should help us explain their ecological effects in these habitats. In this paper I report reproductive data, collected in 1996–1998, on four species of scorpion from southwestern Arizona and southeastern New Mexico: one buthid, *Centruroides exilicauda* (Wood 1863); one diplocentrid, *Diplocentrus peloncillensis* Francke 1975; and two vaejovids, *Pseudouroctonus apacheanus* (Gertsch & Soleglad 1972) and *Vaejovis spinigerus* (Wood 1863). For all, I examined relationships among female size, offspring size, litter size and reproductive investment. I also examined coefficients of variation in offspring size and their relationship to these traits, since offspring size variation may itself be under selection in certain conditions (Kaplan & Cooper 1984; McGinley et al. 1987).

## METHODS

**Study sites and natural history.**—Female scorpions were collected from three sites during 1996 (19–28 May), 1997 (29 June–7 July), and 1998 (21–30 May). All *D. peloncillensis* and *C. exilicauda* were collected from Geronimo Pass (elevation 1770 m) in the Peloncillo Mountains, Hidalgo County, New Mexico, approximately 59 km ENE of Douglas, Arizona (hereafter the Geronimo Pass population, Site 1). All *P. apacheanus* and some *V. spinigerus* were collected in the vicinity of the Southwestern Research Station of the American Museum of Natural History, located in the Chiricahua Mountains southwest of Portal, Cochise County, Arizona (hereafter the SWRS population, Site 2). Elevations ranged from 1620–1800 m. The remainder of the *V. spinigerus* were collected from a stretch of Portal Road (elevation 1370–1420 m) approximately 2–5 km east of Portal (hereafter the Portal population, Site 3). Sites 1 and 2 are primarily Madrean evergreen woodland [Brown 1994a; see Francke (1975) for a further description of the Geronimo Pass site], while site 3 is semidesert grassland (Brown 1994b). Records from SWRS show mean annual precipitation from 1978–1996 was 571 mm, with the wettest months being July and August and the driest months April and May; Geronimo Pass likely shows a similar pattern (Brown 1994a).

Scorpions were collected from under rocks or other surface debris during day searches, or while active on the surface at night by using portable flashlights equipped with ultraviolet bulbs. All females were gravid when collected except for seven *C. exilicauda* found in 1997 with first ($n$ = 5) or second ($n$ = 2) instars on the back. Of the four species studied, *D. peloncillensis* is the only obligate burrower, and was found under rocks at or near the burrow

Table 1.—Extended.

| Total litter mass | Relative litter mass | CV of offspring mass | Instar 1 duration | % Survival |
|---|---|---|---|---|
| 153.2 ± 13.3 | 0.37 ± 0.03 | 10.1 ± 1.9 | 7.4 ± 0.2 | 76.4 ± 7.0 |
| 130.7 ± 13.3 | 0.35 ± 0.04 | 7.9 ± 1.0 | 7.2 ± 0.6 | 89.7 ± 4.9 |
| 472.9 ± 46.1 | 0.56 ± 0.04 | 9.1 ± 1.1 | 8.6 ± 0.6 | 99.7 ± 0.3 |
| 440.7 ± 35.7 | 0.55 ± 0.04 | 9.6 ± 1.0 | 8.9 ± 0.4 | 98.7 ± 1.0 |
| 310.0 ± 35.9 | 0.35 ± 0.03 | 10.4 ± 1.4 | 13.3 ± 0.8 | 92.8 ± 3.0 |
| 44.1 ± 8.3 | 0.30 ± 0.05 | 11.2 ± 3.3 | 7.8 ± 0.5 | 100 ± 0 |

entrance. *Vaejovis spinigerus* is also known to burrow, and at my collecting sites was captured under rocks with and without obvious burrows. The remaining two species inhabit depressions under rocks. *Pseudouroctonus apacheanus* was found only under rocks containing moist soil, and was never captured at night. Conversely, *C. exilicauda* and *V. spinigerus* did not exhibit any noticeable moisture preference and were captured in both day and night searches. Voucher specimens of all species have been deposited at the Denver Museum of Nature and Science.

**Maintenance and data collection.**—Following capture, females were returned to a laboratory at the University of Texas at Arlington, where they were housed individually in 18.5 x 7.5 x 9 cm plastic containers filled with ~0.5 cm of sand. I placed a crumpled paper towel in each container to serve as a refuge; this was kept moistened to increase humidity levels and replaced if it became moldy. I offered each female one adult cricket, *Acheta domestica* (Linnaeus 1758), every third week while gravid (1–2 juvenile crickets for *P. apacheanus*); females carrying offspring were not fed. The laboratory was kept on a 14:10 h light:dark cycle at a mean temperature of 26 °C (range 24–31 °C). Additional heat was provided by heat lamps (100 W incandescent bulbs with a parabolic metal flashing) attached above the shelves holding the plastic containers. I rotated containers daily along the lengths of the shelves to minimize potential effects of temperature variation on embryo development. Previous work (Brown 1998) has demonstrated that using this additional heat source increases parturition success of females and offspring survival to dispersal in the laboratory.

Following birth, first instar juveniles climb onto the female's back, where they undergo their first molt and subsequently disperse. I therefore checked containers daily for the presence of newborns, newly molted second instars or dispersed offspring. For each litter, all offspring molted or dispersed within a single 24 h period. Immediately following dispersal, I weighed the female and all live offspring individually to the nearest 0.1 mg on an analytical balance (Denver Instruments M-220). Litter size equaled the number of living and dead juveniles. Females were then killed by heat shock and preserved in 75% ethanol, after which I measured carapace length (CL), to the nearest 0.1 mm, using a dissecting microscope (American Optical) equipped with an optical micrometer. Using the same procedure I also measured offspring CL on a subset of *C. exilicauda* litters from 1996.

For my measure of reproductive investment I calculated total litter mass (TLM) by summing individual offspring masses. I also calculated a size-corrected measure of investment, relative litter mass (RLM), as TLM divided by female mass. Both TLM and RLM will be underestimated by using masses of second, rather than first, instars, as scorpions lose weight between birth and dispersal (Formanowicz & Shaffer 1993). This is more likely to affect interspecific comparisons since mass loss rates probably vary more among than within species, although the degree to which this is true is unknown. As a measure of within-litter variation in offspring mass I calculated coefficients of variation (CVs) us-

ing the bias correction of Sokal & Rohlf (1995:58). Finally I calculated percent survival of offspring until dispersal as the number of juveniles alive at the time of weighing divided by litter size.

**Data analyses.**—Because they have more space in which to store embryos or are better at obtaining resources, larger females often are predicted to produce more or larger offspring and to have greater reproductive investment. Thus, I examined relationships between female size (CL; see Results) and offspring size, litter size, or TLM using least-squares regression. For the remaining relationships I calculated correlation coefficients (Pearson's $r$), as I had no a priori basis for cause and effect. The trade-off between offspring size and number was examined in the following manner to statistically control for variation in female size. I first regressed offspring mass or litter size against female CL and obtained residuals. I then used these residuals in a correlation analysis. For each species separately, I initially set $\alpha = 0.05$ and then made adjustments using the sequential Bonferroni procedure (Rice 1989) to account for multiple ($n = 10$) significance tests. Regression and correlation results were combined within species for this correction. When $P$ values were less than 0.05 but nonsignificant after Bonferroni correction, I also report adjusted $\alpha$ values.

For *C. exilicauda* I collected sufficient data to make comparisons between years using analysis of variance. Because of statistical problems associated with ratios (Packard & Boardman 1987), in this ANOVA I used the residuals from a regression of TLM on female mass as a measure of RLM. For all analyses reproductive variables were $\log_{10}$-transformed to meet assumptions of parametric tests. Data analysis was carried out using Statistica for Windows version 4.5 (StatSoft 1993).

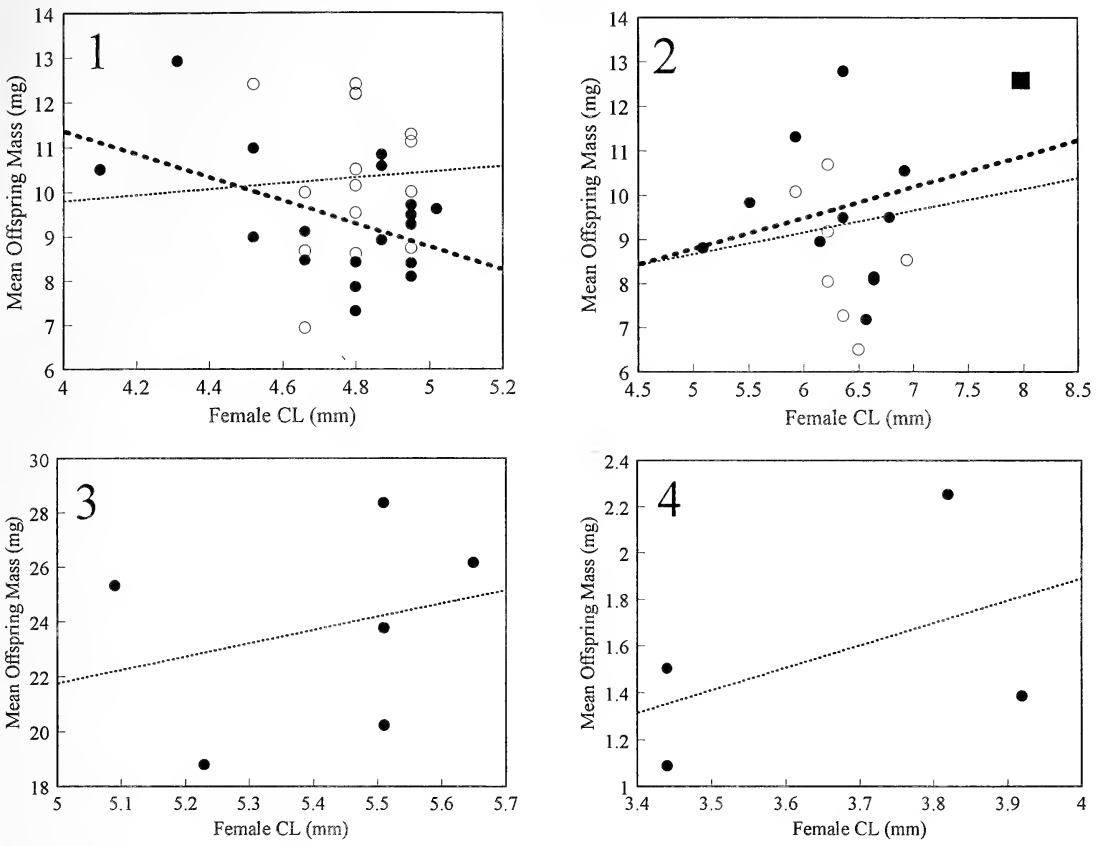
## RESULTS

I obtained data from 63 females, as follows: 33 *C. exilicauda* (1996: $n = 18$; 1997: $n = 15$), 19 *V. spinigerus* (1996 SWRS: $n = 3$; 1996 Portal: $n = 12$; 1997 SWRS: $n = 2$; 1997 Portal: $n = 2$), six *D. peloncillensis* (1996, $n = 4$; 1997: $n = 2$), and five *P. apacheanus* (1996: $n = 1$; 1997: $n = 3$; 1998: $n = 1$). Since relationships among reproductive variables can vary over space or time (e.g., Brown & Formanowicz 1995; Brown 2001), it is preferable to use data from a single population and breeding season. I have therefore examined each year separately for *C. exilicauda* and have calculated two sets of means for *V. spinigerus*, one using all data and one using only 1996 Portal data (which had the largest sample size). For *D. peloncillensis* and *P. apacheanus* I lacked enough individuals in any one year, and so combined data across years. Summary statistics for each species are presented in Table 1.

*Centruroides exilicauda* females gave birth between 13 June–14 July in 1996 and from 1–9 July in 1997. Parturition in both *D. peloncillensis* (16 August–3 September) and *P. apacheanus* (29 July–18 August) occurred later in the season. Portal *V. spinigerus* had the most protracted birthing period, from 30 June–10 August in 1996 (both 1997 females gave birth in mid July). *Vaejovis spinigerus* from SWRS gave birth later than Portal females in both 1996 (10–26 August) and 1997 (2–17 August).

*Diplocentrus peloncillensis* and *V. spinigerus* were similar in mass and the largest species in this study, weighing about twice as much as *C. exilicauda* and 5–6 times more than *P. apacheanus*. However, these differences in female size were not necessarily reflected in other life history traits (Table 1). Offspring of *D. peloncillensis* averaged twice the mass of *V. spinigerus* offspring, while *C. exilicauda* and *V. spinigerus* offspring were similar in mass despite their two-fold difference in adult size. However, *V. spinigerus* had 3–4 times as many offspring as either *D. peloncillensis* or *C. exilicauda*. The smallest species, *P. apacheanus*, also had litters 1.7–2 times larger than *D. peloncillensis* or *C. exilicauda*, albeit with much smaller offspring. Combining offspring size and litter size, *V. spinigerus* invested more in reproduction than the other species, both in absolute (TLM) and relative (RLM) terms. The remaining species, while differing substantially in total investment, had similar RLM values. The per-litter percentage of offspring surviving until dispersal was very high ($\geq 90\%$), with the exception of *C. exilicauda* in 1996. Dead offspring were most often first instars, many of which had died while molting.

*Centruroides exilicauda* did not differ between years in female CL ($F_{1,31} = 0.38$, $P =$




Figures 1–4.—Linear regressions of mean offspring mass against female carapace length for four species of scorpion from Arizona and New Mexico. Regression equations are given in Table 2. Dashed lines indicate a nonsignificant regression. (1) 1996 (filled circles, heavy line) and 1997 (open circles, light line) *Centruroides exilicauda*. (2) 1996 Portal (filled circles, heavy line) and all (filled + open circles, light line) *Vaejovis spinigerus*. The square indicates an outlier (see text). (3) *Diplocentrus peloncillensis*. (4) *Pseudouroctonus apacheanus*.

0.54), offspring mass ($F_{1,31}$ = 2.71, $P$ = 0.11), litter size ($F_{1,31}$ = 3.25, $P$ = 0.08), TLM ($F_{1,31}$ = 1.21, $P$ = 0.28), RLM ($F_{1,31}$ = 0.42, $P$ = 0.52) or within-litter variation in offspring mass ($F_{1,31}$ = 1.23, $P$ = 0.28). However, female mass was significantly greater in 1996 ($F_{1,31}$ = 5.83, $P$ = 0.02). Repeating the above analyses using female mass as the covariate in an ANCOVA again revealed no significant differences among years (results not shown).

Female mass and CL were strongly positively correlated in *V. spinigerus* (1996 Portal: $r$ = 0.87, $P$ < 0.001, $n$ = 12; all females: $r$ = 0.94, $P$ < 0.001, $n$ = 19), *P. apacheanus* ($r$ = 0.96, $P$ = 0.04, $n$ = 4), and *C. exilicauda* in 1996 ($r$ = 0.83, $P$ < 0.001, $n$ = 18). The relationship between these variables was also positive, but not significant, for *D. peloncillensis* ($r$ = 0.60, $P$ = 0.21, $n$ = 6) and *C. exilicauda* in 1997 ($r$ = 0.19, $P$ = 0.49, $n$ = 15). I therefore used CL as my measure of female size because it is less subject to fluctuations (e.g., due to feeding history) than is mass. Results using female mass were qualitatively similar unless otherwise noted. Mass and CL were also significantly positively correlated for *C. exilicauda* offspring in 1996 ($r$ = 0.75, $P$ = 0.01, $n$ = 10), and I therefore report only correlations involving mass (using CL gave similar results) to be consistent with the 1997 data.

For *C. exilicauda*, *D. peloncillensis*, and *P. apacheanus*, female size was uncorrelated with offspring size, litter size, or total investment following Bonferroni correction (Table 2; Figs. 1, 3–5, 7–9, 11, 12). For *C. exilicauda*, marginally significant positive correlations were found between female size and litter size

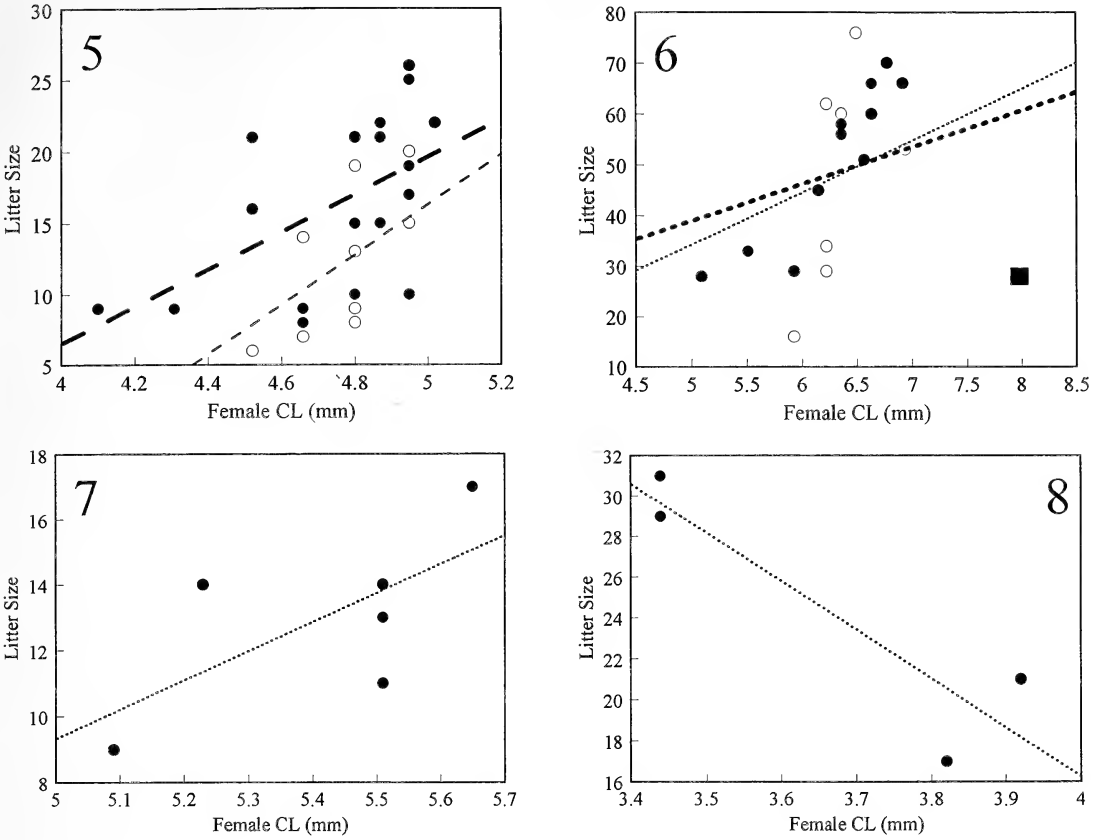
Table 2.—Linear regression statistics for the relationship between female size (carapace length) and offspring mass (OM), litter size (LS), or total litter mass (TLM) for four species of scorpion from Arizona and New Mexico. All variables were log-transformed prior to analysis. df = degrees of freedom for the *F*-test.

| Species | Variable | Slope | Intercept | $R^2$ | *F* | *P* |
|---|---|---|---|---|---|---|
| 1996 *C. exilicauda* | OM | −1.17 | 4.06 | 0.21 | 4.28 | 0.055 |
| df = 1, 16 | LS | 4.10 | −3.67 | 0.31 | 7.08 | 0.017 |
| | TLM | 2.93 | 0.39 | 0.15 | 2.80 | 0.11 |
| 1997 *C. exilicauda* | OM | 0.54 | 1.47 | 0.007 | 0.10 | 0.76 |
| df = 1, 13 | LS | 7.62 | −9.46 | 0.32 | 5.99 | 0.029 |
| | TLM | 8.16 | −7.99 | 0.31 | 5.83 | 0.031 |
| 1996 Portal *V. spinigerus* | OM | 0.36 | 1.61 | 0.05 | 0.56 | 0.47 |
| df = 1, 10 | LS | 1.16 | 1.70 | 0.13 | 1.56 | 0.24 |
| | TLM | 1.51 | 3.30 | 0.25 | 3.32 | 0.10 |
| All *V. spinigerus* | OM | 0.20 | 1.85 | 0.01 | 0.18 | 0.68 |
| df = 1, 17 | LS | 1.73 | 0.60 | 0.15 | 2.88 | 0.11 |
| | TLM | 1.93 | 2.45 | 0.22 | 4.79 | 0.042 |
| *D. peloncillensis* | OM | 1.11 | 1.29 | 0.08 | 0.33 | 0.60 |
| df = 1, 4 | LS | 3.86 | −3.98 | 0.47 | 3.60 | 0.13 |
| | TLM | 4.97 | −2.68 | 0.49 | 3.84 | 0.12 |
| *P. apacheanus* | OM | 2.24 | −2.49 | 0.26 | 0.70 | 0.49 |
| df = 1, 2 | LS | −3.64 | 7.89 | 0.79 | 7.51 | 0.11 |
| | TLM | −1.40 | 5.39 | 0.21 | 0.53 | 0.54 |

in both years (1996: $P = 0.017$, adjusted $\alpha = 0.0056$; 1997: $P = 0.029$, adjusted $\alpha = 0.0056$) and between female size and TLM in 1997 ($P = 0.031$, adjusted $\alpha = 0.0063$). The regressions involving litter size and TLM for *C. exilicauda* in 1997 were in the same direction when female mass was used in place of CL, but were much weaker and not significant (log litter size = 1.4 + 0.18*log female mass, $R^2 = 0.002$, $F_{1,13} = 0.03$, $P = 0.86$; log TLM = 2.9 + 0.32*log female mass, $R^2 = 0.007$, $F_{1,13} = 0.09$, $P = 0.77$). Surprisingly, both litter size and TLM declined with increasing female size in *P. apacheanus*.

Female size was also uncorrelated with reproductive traits in *V. spinigerus* after Bonferroni correction (Table 2; Figs. 2, 6, 10), although there was a marginally significant relationship between female size and TLM when using data from all litters ($P = 0.042$, adjusted $\alpha = 0.0063$). However, one data point (the square in Figs. 2, 6, 10) was determined to be an outlier. With this removed there was no change in the relationship between female size and offspring mass (results not shown), but both litter size and TLM were now significantly positively correlated with female size (litter size: 1996 Portal: log litter size =−2.13 + 3.28*log female CL, $R^2 = 0.84$, $F_{1,9} = 44.9$, $P < 0.0001$; all females: log litter size = −3.02 + 3.72*log female CL, $R^2 = 0.48$, $F_{1,16} = 14.5$, $P = 0.002$; TLM: 1996 Portal: log TLM = 0.41 + 3.12*log female CL, $R^2 = 0.69$, $F_{1,9} = 19.8$, $P = 0.002$; all females: log TLM = −0.05 + 3.31*log female CL, $R^2 = 0.43$, $F_{1,16} = 12.0$, $P = 0.003$).

Reproductive investment, measured as TLM, was uncorrelated with offspring mass in all species (Table 3; Figs. 13–16), although greater investment tended to be associated with larger offspring in *D. peloncillensis* and *P. apacheanus*. Offspring number was significantly positively correlated with TLM in *C. exilicauda* and *V. spinigerus*, and the correlation between these traits was marginally positive in *D. peloncillensis* ($P = 0.04$, adjusted $\alpha = 0.005$; Table 3; Figs. 17–20). I found no evidence of a trade-off between offspring size and number (Figs. 21–24) in *C. exilicauda* (1996: $r = 0.21$, $P = 0.40$, $n = 18$; 1997: $r = -0.12$, $P = 0.68$, $n = 15$), *P. apacheanus* ($r = -0.74$, $P = 0.26$, $n = 4$), or *D. peloncillensis* ($r = -0.18$, $P = 0.73$ $n = 6$). There was also no trade-off in the 1996 Portal *V. spinigerus* ($r = -0.45$, $P = 0.14$, $n = 12$), although a marginally significant trade-off was found when including all data ($r = -0.50$, $P = 0.03$, adjusted $\alpha = 0.0056$, $n =$

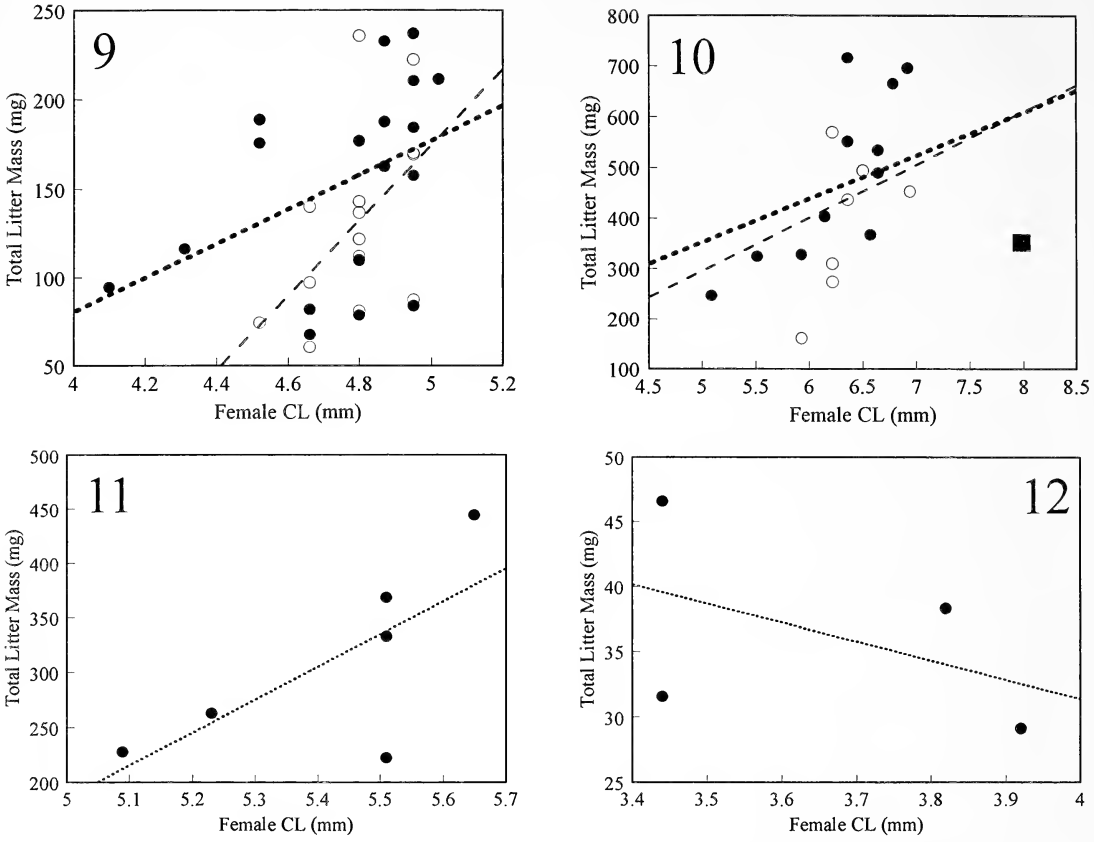



Figures 5–8.—Linear regressions of litter size against female carapace length for four species of scorpion from Arizona and New Mexico. Regression equations are given in Table 2. Short dashed lines indicate a nonsignificant regression, long dashed lines a marginally significant regression. Symbols as in Figure 1. (5) *Centruroides exilicauda*. (6) *Vaejovis spinigerus*. (7) *Diplocentrus peloncillensis*. (8) *Pseudouroctonus apacheanus*.

19). Within-litter variation in offspring mass (CV) was uncorrelated with other traits in most species (Table 3); the only exceptions were marginally negative correlations between CV and litter size ($P = 0.044$, adjusted $\alpha = 0.0063$) or TLM ($P = 0.026$, adjusted $\alpha = 0.0056$) for the 1996 Portal *V. spinigerus*. No obvious trends were found in CV patterns across species. Removal of the outlier for *V. spinigerus* qualitatively altered none of the above results (results not shown).

Captivity is suspected to affect scorpion reproduction because of differences in prey availability or environmental parameters between the field and laboratory (Polis & Sissom 1990). Therefore, for each species I examined correlations between days in captivity (the time between capture and parturition) and female mass, offspring mass, litter size, and total litter mass, the traits most likely to be affected by laboratory conditions. Within a species, these traits tended to either all increase or all decrease (Table 4), although there was no consistent overall pattern across species. Only two correlations were marginally significant: litter size of *V. spinigerus* (all litters; $P = 0.05$, adjusted $\alpha = 0.0125$), and mass of female *C. exilicauda* in 1997 ($P = 0.04$, adjusted $\alpha = 0.0125$), declined with time spent in captivity. The results for *C. exilicauda* are likely unimportant, as all litters had dispersed within 18 days of capture.

Both *C. exilicauda* females captured in 1997 carrying second instar juveniles gave birth in the laboratory to a second litter. The times between dispersal of the first litter and birth of the second were 109 and 341 days. Both females increased substantially (93–94




Figures 9–12.—Linear regressions of total litter mass against female carapace length for four species of scorpion from Arizona and New Mexico. Regression equations are given in Table 2. Short dashed lines indicate a nonsignificant regression, long dashed lines a marginally significant regression. Symbols as in Figure 1. (9) *Centruroides exilicauda*. (10) *Vaejovis spinigerus*. (11) *Diplocentrus peloncillensis*. (12) *Pseudouroctonus apacheanus*.

mg) in post-dispersal mass and produced larger second litters (first litter/second litter: 8/18 and 13/14). Mean offspring mass in the second litter increased for one female and decreased for the other (10.1 mg/8.9 mg and 10.5 mg/11.8 mg, respectively, for the litter sizes above). Neither female had access to males after capture, but I do not know whether females had remated in the field while gravid or whether sperm from a single mating was used for both litters.

## DISCUSSION

Based on data summarized in Polis & Sissom (1990) and Brown (2001), *V. spinigerus* had larger litters than other species in the family Vaejovidae [mean = 27.5 ($n$ = 22)] or the genus *Vaejovis* [mean = 29.0 ($n$ = 10)]. Previous authors have reported litter sizes of 13–69 for *V. spinigerus* ($n$ = 4 litters; McAlister 1960; Stahnke 1966; Williams 1969); two Portal females had litters larger than this maximum (70 and 76 juveniles). First instar duration was shorter than the family mean of 12.6 d ($n$ = 8), but slightly longer than the duration reported for *V. spinigerus* by McAlister (1960; 7–8 d).

In contrast, both *C. exilicauda* and *D. peloncillensis* had smaller litters on average than other confamiliars [Buthidae mean = 22.8 ($n$ = 33), Diplocentridae mean = 24.6 ($n$ = 8)] or congeners [*Centruroides* mean = 37.5 ($n$ = 7), *Diplocentrus* mean = 24.8 ($n$ = 6)]. Geronimo Pass *C. exilicauda* had litters intermediate in size to those of inland (mean = 10.1) and coastal (mean = 18.2) *C. exilicauda* from Baja California [Myers 2001; however, this likely represents a distinct species from the New Mexico population (Gantenbein et al. 2001)], but smaller than the mean of 20 for

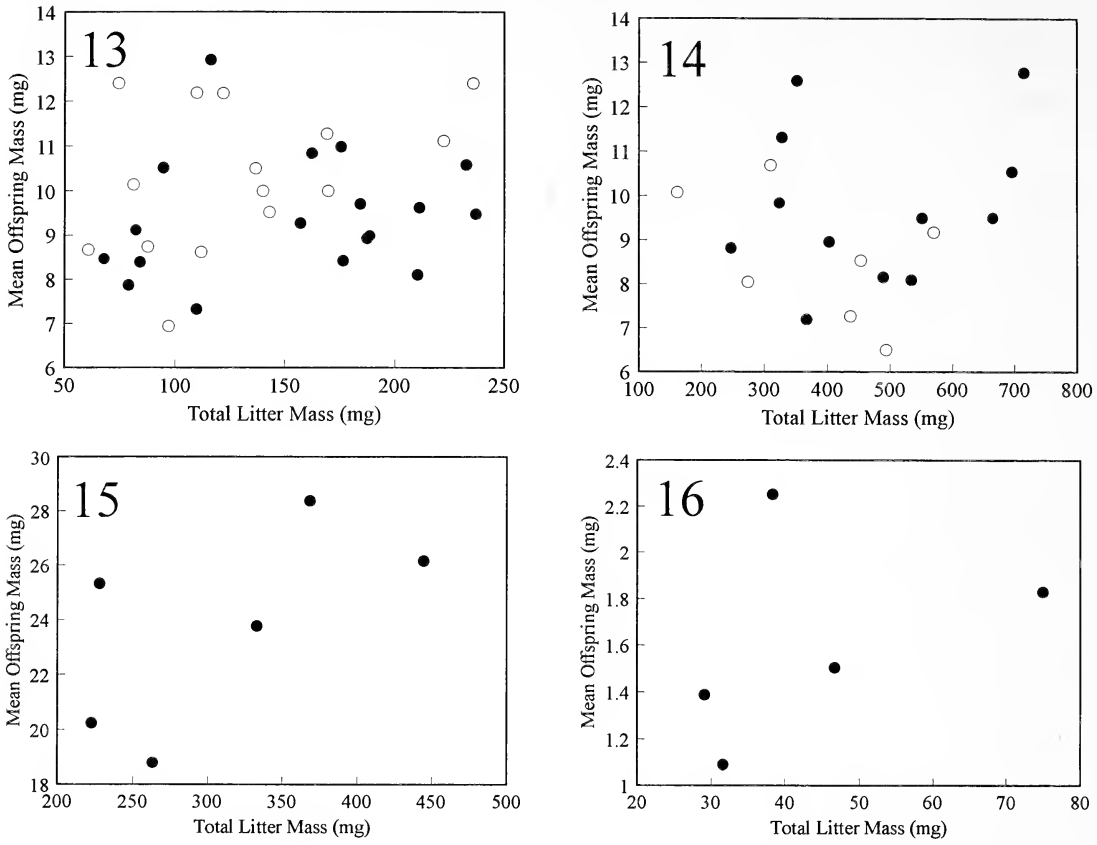
Table 3.—Correlations (Pearson's $r$) between reproductive traits in four species of scorpion from Arizona and New Mexico. FCL = female carapace length. All other abbreviations are defined in Tables 1 and 2. * $P < 0.05$, *** $P < 0.001$.

| | Correlation between: | | | | | |
|---|---|---|---|---|---|---|
| | TLM-OM | TLM-LS | CV-FCL | CV-OM | CV-LS | CV-TLM |
| 1996 *C. exilicauda* ($n$ = 18) | 0.24 | 0.94*** | 0.37 | −0.36 | −0.20 | −0.31 |
| 1997 *C. exilicauda* ($n$ = 15) | 0.38 | 0.90*** | 0.40 | −0.07 | 0.06 | 0.03 |
| 1996 Portal *V. spinigerus* ($n$ = 12) | 0.17 | 0.88*** | −0.29 | −0.05 | −0.59* | −0.64* |
| All *V. spinigerus* ($n$ = 19) | 0.004 | 0.90*** | −0.20 | −0.34 | −0.13 | −0.30 |
| *D. peloncillensis* ($n$ = 6) | 0.61 | 0.83* | −0.20 | 0.04 | 0.17 | 0.15 |
| *P. apacheanus* ($n$ = 5) | 0.48 | 0.71 | −0.32 | −0.86 | 0.13 | −0.52 |

this species (Polis & Sissom 1990). First instar duration was similar to family means for *C. exilicauda* [mean = 6.5 d ($n$ = 20)] and *D. peloncillensis* [mean = 14.4 d ($n$ = 4)], and for *C. exilicauda* was within the range previously reported for this species (6–15 d: Stahnke 1966; Williams 1969). *Pseudouroctonus* life history data are available for only a single litter of *P. reddelli* (Gertsch & Soleglad 1972). This species is much larger than *P. apacheanus* and has larger litters and a slightly shorter first instar duration (Brown 1997).

With the exception of *V. spinigerus*, relative litter mass was lower than in any sexually reproducing scorpion (range 0.44–0.55: Benton 1991a; Formanowicz & Shaffer 1993; Brown & Formanowicz 1995, 1996; Lourenço et al. 1996). Such low relative investment might occur if females cannibalize some newborns, decreasing observed litter sizes. However, no females in this study were observed feeding on juveniles. Low food levels might also lead females to invest fewer resources in reproduction, or to resorb some embryos (Polis & Sissom 1990). If precipitation levels can be used as a proxy for arthropod prey availability, then reduced investment might be expected in 1996, when only 27.4 mm of precipitation had fallen by the end of May when scorpions were collected. However, RLM was as low in 1997 (e.g., for *C. exilicauda*), when > 7 times as much rain (202.4 mm) had fallen in the same period. Conditions in the laboratory might also have been more stressful than in the field, leading to decreased investment in reproduction (lower TLM), maintenance (lower female mass), or both, as time spent in captivity increased. If so, low RLM should primarily reflect declines in TLM, a trend not supported by my data for any species. Thus, relatively low reproductive investment in *C. exilicauda, D. peloncillensis,* and *P. apacheanus* may simply reflect an adaptive response by these species to specific environmental conditions, such as a decrease in the length of the growing season or lower prey availability, in lower montane woodlands. Obviously, more comparative investment data for scorpions from various habitats are required to assess this hypothesis.

For *C. exilicauda* and *D. peloncillensis*, more detailed comparisons can be made to *C. vittatus* (Say 1821) and *D. lindo* Stockwell & Baldwin 2001. The latter two species occur sympatrically at Chandler Independence Creek Preserve in west Texas (Brown & Formanowicz 1995, 1996), which differs in elevation (~700 m) and habitat (Chihuahuan desert scrub) from Geronimo Pass. Reproductive data were obtained for the Texas species in 1992 (Brown & Formanowicz 1995, 1996) and 1996–1997 (Brown unpub. data). *Diplocentrus* females are similar in size, while *C. vittatus* females are ~30% larger by mass than *C. exilicauda* females. For the other reproductive traits, the same pattern emerged for each




Figures 13–16.—Correlations between total litter mass and mean offspring mass for four species of scorpion from Arizona and New Mexico. Correlation coefficients are given in Table 3. Symbols as in Figure 1. (13) *Centruroides exilicauda*. (14) *Vaejovis spinigerus*. (15) *Diplocentrus peloncillensis*. (16) *Pseudouroctonus apacheanus*.

congener pair: Texas scorpions had larger litters, smaller offspring, and larger total and relative investment than New Mexico scorpions (part of this trend was relaxed for *D. lindo* in 1997, as TLM and RLM were just slightly larger than comparable values for *D. peloncillensis*).

The proximate cause of these interspecific differences is unknown, given that the two study sites differ in a number of environmental characteristics. For instance, temperature is known to affect growth rates, adult size, and reproduction in a variety of ectotherms (e.g., Li & Jackson 1996; Ernsting & Isaaks 2000). In particular, theoretical and empirical studies (e.g., Yampolsky & Scheiner 1996; Ernsting & Isaaks 2000) have demonstrated that egg/offspring size decreases, and litter size increases, with an increase in temperature. Decreases in offspring size may not balance increases in offspring number, so that total investment may be greater at higher temperatures (Ernsting & Isaaks 2000). Given that mean and maximum monthly temperatures are higher at Independence Creek than Geronimo Pass across the year [using data from the southern (NCDC 2002a) and western (NCDC 2002b) regional climate center websites, respectively], the trends for *Centruroides* and *Diplocentrus* are in the predicted direction. Alternatively, larger offspring size may be favored at Geronimo Pass if predation pressure on juveniles is greater or food availability for juveniles is lower than at Independence Creek. Under such conditions large offspring are predicted to survive better and/or develop faster than small offspring (Shine 1978; Itô & Iwasa 1981).

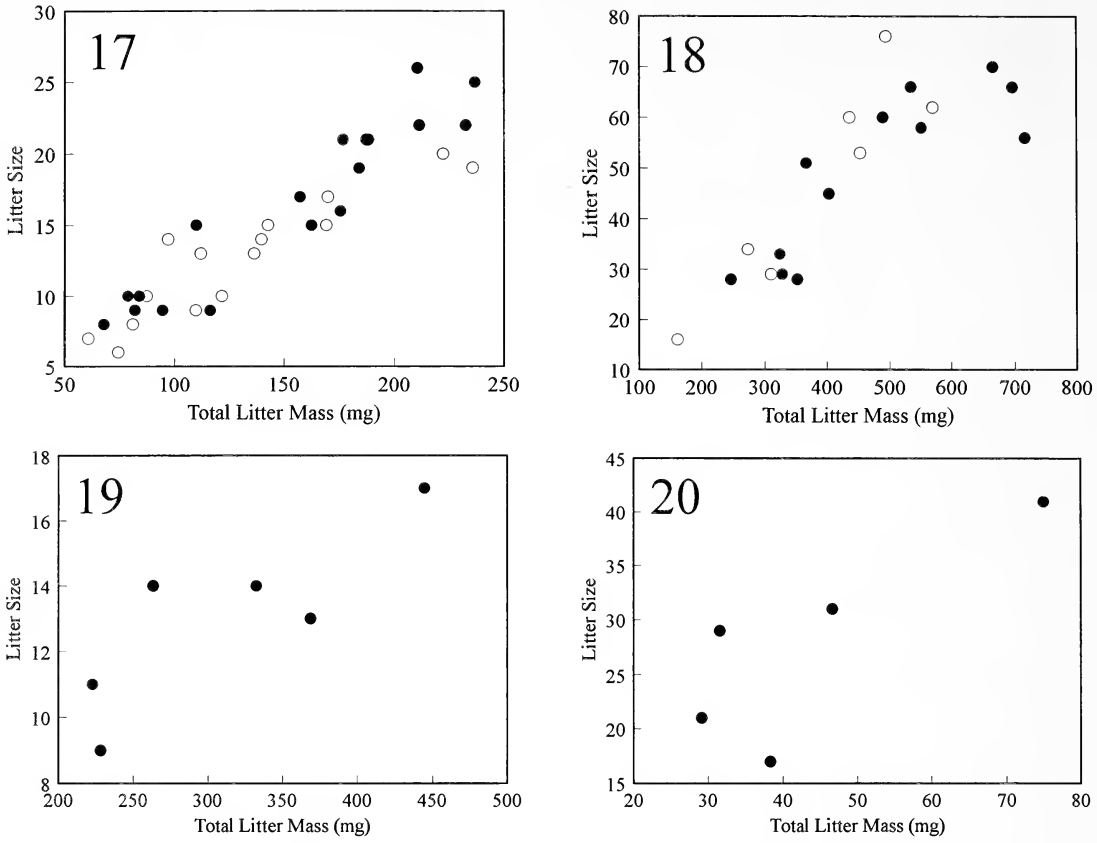
Female size had little influence on offspring size, but larger females tended to have larger

Table 4.—Correlations (Pearson's $r$) between days spent in captivity and selected reproductive traits in four species of scorpion from Arizona and New Mexico. All abbreviations are defined in Tables 1 and 2. * $P < 0.05$.

| | Correlation between days in captivity and: | | | |
|---|---|---|---|---|
| | Female mass | OM | LS | TLM |
| 1996 *C. exilicauda* ($n$ = 18) | 0.40 | −0.14 | −0.30 | −0.34 |
| 1997 *C. exilicauda* ($n$ = 15) | −0.54* | 0.17 | 0.35 | 0.39 |
| 1996 Portal *V. spinigerus* ($n$ = 12) | 0.15 | −0.05 | −0.44 | −0.48 |
| All *V. spinigerus* ($n$ = 19) | −0.01 | 0.33 | −0.46* | −0.35 |
| *D. peloncillensis* ($n$ = 6) | 0.75 | 0.47 | 0.40 | 0.58 |
| *P. apacheanus* ($n$ = 5) | 0.54 | 0.71 | 0.16 | 0.66 |

litters and invest more into reproduction in all species but *P. apacheanus*. The latter two relationships are somewhat equivocal, as the correlations between female size and litter size or TLM were nonsignificant (for *D. peloncillensis*), marginally significant (for *C. exilicauda*), or significant only after removal of an outlier (for *V. spinigerus*). Nevertheless, these trends are likely to reflect real and biologically meaningful relationships, given that a positive correlation between female size and litter size or total investment is common in other taxa (reviewed in Roff 1992; Stearns 1992), including other arachnids (e.g., solifuges: Punzo 1998; spiders: Kessler 1971; Killebrew & Ford 1985; McLay & Hayward 1987; Punzo & Henderson 1999). In a recent review, Brown (2001) examined allometric relationships involving offspring size or number for 11 species of scorpion (including three of the four current species), some represented by multiple populations or years. Adding two additional sources (Formanowicz & Shaffer 1993; Myers 2001), significant positive correlations with female size (measured as mass in most cases) were found in only six of 30 cases for offspring size (with two additional significant negative correlations) and 12 of 32 cases for litter size (with one significant negative correlation). Total litter mass appears to correlate more strongly with female size for scorpions in general, as in six of eight previous cases this relationship was at least marginally significant (Bradley 1984; Benton 1991b; Formanowicz & Shaffer 1993; Brown & Formanowicz 1995, 1996). Thus, my results agree in general with those from previous studies of scorpion reproduction, although my support for an allometric effect on litter size was stronger than in Brown (2001).

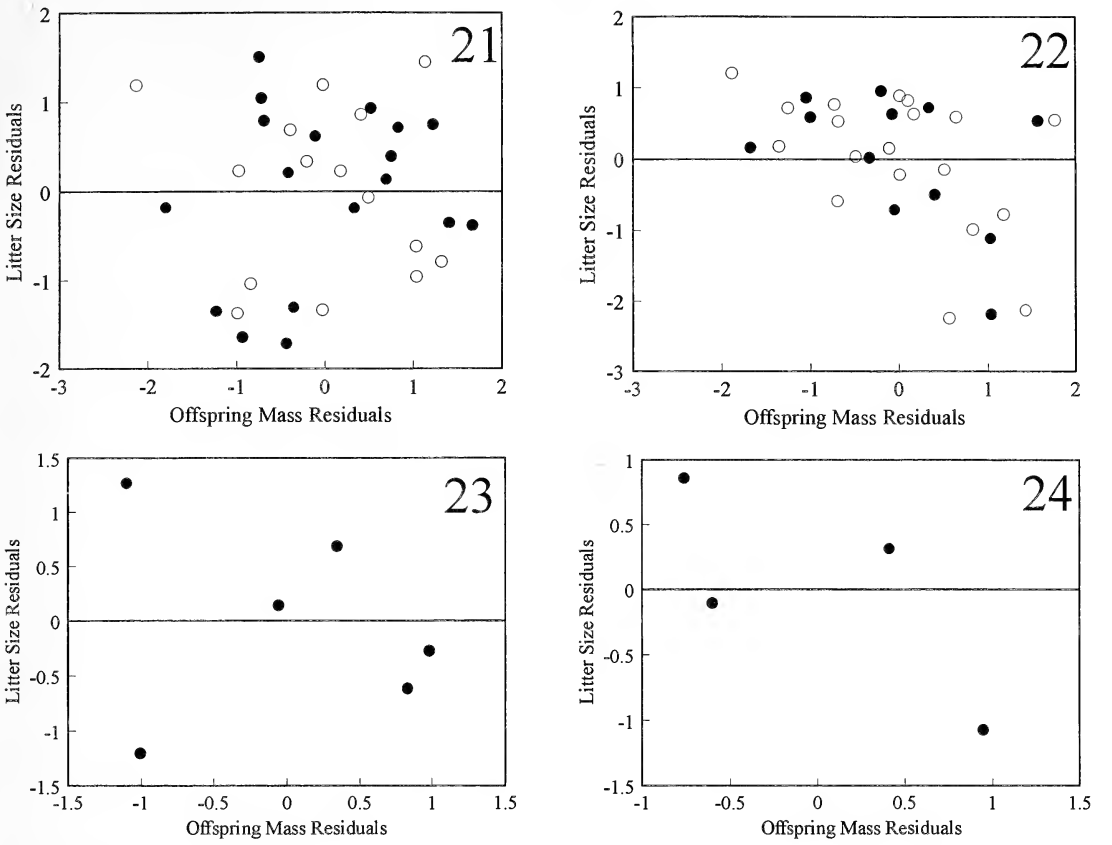
In the current study and in Brown (2001), two issues may obscure detection of significant allometric effects. First, sample sizes may be too low to reveal effects; for example, in the current study the significant or marginally significant results involving litter size and TLM came from the two species (*C. exilicauda* and *V. spinigerus*) with the largest sample sizes. The use of Bonferroni correction, although conceptually justified, may exacerbate this problem by making it harder to detect important trends. I note, however, that across species of scorpions sample size is uncorrelated with the magnitude of the correlation coefficient between female size and litter size [$r$ = 0.005, using data from Brown (2001)]. Second, and perhaps more importantly, the choice of female size measure appears to alter the strength of the correlation with litter size (and TLM) in a usually consistent way. In the current study, in all cases litter size was more strongly correlated with female CL ($R^2$ range without removing *V. spinigerus* outlier, 0.13–0.79) than with female mass ($R^2$ range, 0.002–0.12), although only for 1997 *C. exilicauda* did statistical significance change. The same




Figures 17–20.—Correlations between total litter mass and litter size for four species of scorpion from Arizona and New Mexico. Correlation coefficients are given in Table 3. Symbols as in Figure 1. (17) *Centruroides exilicauda*. (18) *Vaejovis spinigerus*. (19) *Diplocentrus peloncillensis*. (20) *Pseudouroctonus apacheanus*.

trend holds in *Tityus columbianus* (Thorell 1876), where litter size is strongly correlated with female body length but weakly correlated with female mass (Lourenço et al. 1996), and *C. vittatus*, where litter size and TLM are more strongly correlated with female CL than female mass in seven of ten population-year combinations (Brown 1998). Thus, female mass may be a relatively poor measure for examining allometric relationships in scorpions, and significant correlations between litter size and female size may be more common than reported in Brown (2001).

The lack of significant relationships between offspring size and female size or TLM suggests that offspring size is relatively canalized compared to litter size. This was reflected in coefficients of variation across females; CVs of litter size (range of species means, 21.2–42.5%) were 1.5–3 times greater than CVs of offspring size (range, 14.2–27.6%). My results are consistent with those from other terrestrial ectotherms (e.g., lizards: Congdon 1989; spiders: Kessler 1971; McLay & Hayward 1987; Killebrew & Ford 1985; insects: Mappes et al. 1996; scorpions: Brown & Formanowicz 1995, 1996; Lourenço et al. 1996) indicating that increases in reproductive output result primarily from adding offspring rather than increasing offspring size. Canalization of offspring size may represent a decision by females to allocate a relatively constant amount of resources to each offspring. As suggested for spiders (Marshall & Gittleman 1994), this amount may be near the minimum necessary to ensure survival of offspring until dispersal. Variation in offspring size among or within litters might then reflect "noise" created by a female's inability to precisely allocate resources. Alternatively, the




Figures 21–24.—Correlations between residual offspring mass and residual litter size for four species of scorpion from Arizona and New Mexico. Correlation coefficients are given in the text. Symbols as in Figure 1. (21) *Centruroides exilicauda*. (22) *Vaejovis spinigerus*. (23) *Diplocentrus peloncillensis*. (24) *Pseudouroctonus apacheanus*.

relative uniformity in offspring size may reflect anatomical constraints (see e.g., Congdon & Gibbons 1987), perhaps in the structure of the ovariuterus or genital operculum, which limits egg or offspring size but is unrelated itself to female size.

I found little support for an offspring size-number trade-off in the four species studied, similar to the trend for scorpions in general (Brown 2001). Also similar to results from other arachnids (Simpson 1993; Brown 1998, 2001) was the year-to-year change in strength and magnitude of the trade-off in *C. exilicauda*. The reasons for this are unclear, as much life history theory predicts that offspring size and number will be negatively correlated if resources available for reproduction are limited (Roff 1992, 2002; Stearns 1992). Variation in acquisition of resources, which can occur if better quality females obtain more or better quality prey, has been predicted to potentially obscure trade-offs between offspring size and number (van Noordwijk & de Jong 1986). Brown (in press) has recently demonstrated that this hypothesis applies to scorpions, that is, that stronger (more significant) negative correlations between offspring size and number occur when variation among females in reproductive investment (a measure of variation in resource acquisition by females) is relatively low. A second explanation for the lack of a trade-off involves the relatively constant size of offspring. If there exists a fixed allocation strategy, that is, females use their reproductive resources to make as many offspring as possible of a given (minimal?) size, then there is no underlying basis for a trade-off.

In summary, I found little evidence for larger females to produce larger offspring for any

of the species studied. However, for two of the four species (*C. exilicauda* and *V. spinigerus*) larger females produced more offspring and had a greater total litter mass, although these results were not always significant after Bonferroni correction. For each of the four species studied, females with higher reproductive investment produced more but not larger offspring than females with lower investment. Finally, no trade-off existed between offspring size and number, except when I combined data across years and populations in *V. spinigerus*. These results do not appear to be unusual among scorpions, and understanding the generality of these patterns and the factors that influence them remains a major challenge to scorpion biologists. Experiments in which environmental factors such as prey availability or temperature are manipulated and reproductive traits measured are the next critical step.

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# POPULATION DYNAMICS OF AN ISOLATED POPULATION OF THE HARVESTMAN *ILHAIA CUSPIDATA* (OPILIONES, GONYLEPTIDAE), IN ARAUCARIA FOREST (CURITIBA, PARANÁ, BRAZIL)

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**ABSTRACT.** The harvestman *Ilhaia cuspidata* was studied in Curitiba, state of Paraná, Brazil. The site studied is a 30,000 m$^2$ forest remnant of *Araucaria* forest surrounded by houses. Harvestmen were sampled 21 times over 14 months (June 1997–August 1998); at intervals of 21–30 days. The population size was estimated by Fisher-Ford and Jolly methods, and did not vary considerably from autumn (June) to spring (November 1997). However, it increased rapidly (300 %) during late spring and summer (December–March). The lowest population size estimated was 1,429 adults/subadults, during the winter (June 1997) and, the highest was 14,445 during the autumn (April 1998). The recapture rates ranged from 16%–41%. The sex ratio observed in all sampling periods was 1:1. The density varied from 0.05 (winter) to 0.47 adult + subadults/m$^2$ (autumn). The extremely different abundances observed between seasons could have been influenced by temperature. The immatures were observed all year, suggesting a continuous reproduction, but they were much more abundant during spring and summer. Ecological aspects including aggregation, individual movement and life span were also discussed.

**Keywords:** *Araucaria* forest, *Ilhaia cuspidata*, Opiliones, Population ecology

Harvestmen are normally solitary, nocturnal, omnivores, vagile and photophobic (Coddington et al. 1990; Savory 1938). They are commonly found in humid forests, under fallen trunks, in leaf litter, mosses and inside caves (Edgar 1990). Members of this order are very common in Neotropical forests, where their diversity can be very high, in the Atlantic Rain Forest of Brazil, more than one harvestmen can be found per square meter (Pinto-da-Rocha pers. obs.). In temperate zones harvestmen biomass sometimes can exceed that of spiders and they may be important controllers of insect populations (Hillyard & Sankey 1989).

Data on population biology and the natural history of Opiliones in South America are very scarce (see Gnaspini 1996; and Pinto-da-Rocha 1999 for references). Specific studies related to the ecology and population biology of Neotropical harvestmen have been conducted with *Goniosoma spelaeum* (Mello-Leitão 1933) (Gonyleptidae, Goniosomatinae) in caves of the Ribeira valley, São Paulo, Brazil (Gnaspini 1996), *Pachylospeleus strinatii* Silhavý 1974 in the "Gruta das Areias de Cima", São Paulo, Brazil (Pinto-da-Rocha 1996a), *Daguerreia inermis* Soares & Soares 1947 in the "Gruta da Lancinha", Paraná, Brazil (Pinto-da-Rocha 1996b), and *Pachyloidellus goliath* Acosta 1993 in "Pampa de Achala", Córdoba, Argentina (Acosta et al. 1995).

In southeastern Brazil, the composition of harvestmen fauna of the Atlantic Rain Forest is different in each mountain chain and more than 50 species can be found in each area of endemism (Pinto-da-Rocha 1999). Most species are endemic, occupying small areas, normally one mountain chain or some caves (Pinto-da-Rocha 1999). The cavernicolous harvestmen do not vary in abundance through the year, and their populations seem to be more stable than epigean populations (Gnas-

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pini 1996; Pinto-da-Rocha 1996a; 1996b), probably because epigean climates are more variable than inside caves. Thus, we expect that epigean harvestmen populations will vary in abundance through the year.

The epigean species *Ilhaia cuspidata* Roewer 1913 has a wide distribution, occurring in southern to southeastern Brazil from the state of Rio de Janeiro to Paraná. It inhabits leaf litter of subtropical humid forests and synantropic environments, such as second growth and forest fragments inside cities. In this study we examinate the population dynamics and intra and interspecfic interactions of this harvestmen species in an urban site, intending to understand possible seasonal variations in abundance and other biological aspects.

## METHODS

**Study site (Fig. 1).**—This study was carried out in an Araucaria forest fragment, located in the "Museu de História Natural do Capão da Imbuia" east of Curitiba county, Brazil (25′25″48°S, 49′16″15°W). This forest fragment comprises 30,000 m² that was isolated in the last 50–70 years and today is surrounded by houses, prior the park foundation. The Araucaria forests in south Brazil are characterized by trees averaging 25–30 m high, with great biomass of large Gymnospermae *Araucaria angustifolia* (Bertol. 1898.) Kuntze. Open understories are dominated by shrubs and vines, and in secondary forests, the case of this study, the ground is mainly covered by leaves and fallen trees, where harvestmen can live. Subtropical Humid Mesotermic characterizes the climate of the region, with a warm season and a cold season with frequent frosts (May–September). The mean temperature in the warm season is below 22 °C and in the coldest months are below 12 °C. The annual mean is 17 °C. Rainfall is between 1300 and 1500 mm per year (105–190 mm each month from September–March and 78–102 mm from April–August) and relative humidity averages 85% (Mack 1981) (Fig. 2). The meteorological data (Fig. 2) used in this study were obtained from the "Estação Meteorológica do Centro Politécnico" (located 5 km from the study site) supplied by the "Sistema Meteorológico do Paraná (SIMEPAR)".

**Capture-recapture.**—Individual harvestmen were collected from June 1997 to August of 1998 by one person, during daylight, with intervals of 21–30 days between each one of the 21 samples. The time spent in the field taking samples varied from 5–16 h, depending on the total number of captured animals. The study site was arbitrarily divided into 23 sampling points of strips of 100 m² (Fig. 1). At each sample point all harvestmen were carefully collected (under fallen trunks, boards, bricks, etc.) with forceps and a flashlight for searching in crevices. All adults and last nymphal stages (i.e., harvestmen without arolium, see Munõz-Cuevas 1971) encountered were captured. The immature stages of *I. cuspidata* Roewer 1913 and other harvestmen species observed were counted, but not captured or marked. After capture, the harvestmen (adults and last nymphal stages) were sexed (differentiated mainly by heavy armature of male leg IV, weak on females), counted and marked with acrylic or plastic ink on the back region of the dorsal scute or on the femora of the fourth leg in specific combinations of colors for each sample date. This ink did not harm the individuals and after several recaptures the marks were still easily recognizable (see Appendix 1). The marked individuals were released at the same place where they were collected. Voucher specimens were deposited in the Museu de Zoologia da Universidade de São Paulo and Museu de História Natural "Capão da Imbuia".

**Shelter preferences.**—The 23 sample points were characterized on the basis of the quantity of possible shelters present in each sample site (100 m²) that could be influencing the local abundance of harvestmen. The shelters were classified in 4 categories for subsequent statistical analysis: trunks, stones, bricks and trash (objects of inorganic origin, plastic objects). We compared separately the number of adult harvestmen observed per sample point, in habitats with high (H), medium (M) and low (L) concentration of different shelters by Kruskal-Wallis and Dunn's Tests.

**Behavioral observations.**—Prior to our population study we collected harvestmen on three dates (21 March, 11 April and 5 May 1997). At these times captured individuals were individually marked with a small drop of acrylic ink. These data were not considered in the estimates of population size, but they were used for observations of individual movements. During each sample period we re-

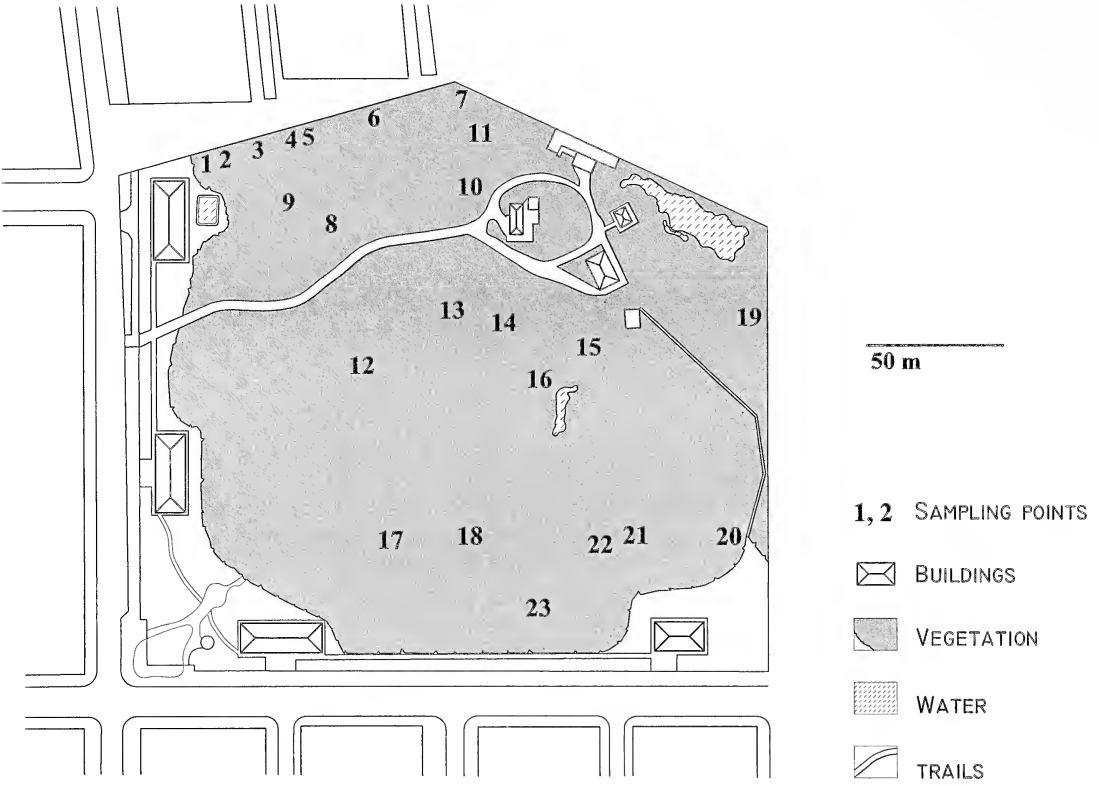


Figure 1.—Map of the study site, Curitiba, Brazil.

corded the number and sex of aggregated individuals. We considered as "aggregated" harvestmen that had legs in contact with one or more others harvestmen. We established five categories of aggregations: (a) males only, (b) females only, (c) both males and females, (d) males, females and immatures and (e) multi-species aggregations, with individuals of *I. cuspidata* and other harvestmen species. We analyzed differences between numbers of individuals in aggregates by seasons. We made two night observations in the study site (on 20 March and 13 July 1998). We counted the active individuals observed in a 100 m transect (width 5 m), in periods of 15 minutes, from 1700 h–2000 h. Behavioral and foraging observations were made in a hexagonal terrarium of glass (50 x 40 cm) with approximately 2 cm of soil, three shelters and two plastic receptacles with water. This terrarium housed 13 individuals of *Ilhaia cuspidata*, one female of *Discocyrtus* sp.2, one male of the spider *Polybetes pitagoricus* (Holmberg 1875) (Araneae, Sparassidae), one female of the spider *Ctenus* sp. (Araneae, Ctenidae) and two diplopods. Also included were crickets, cockroaches, isopods and slugs.

**Statistical methods.**—The population size of *I. cuspidata* was estimated by Fisher-Ford and Jolly algorithms (Begon 1979). Both methods require several phases of marks and recaptures. In the Fisher-Ford method, the population size is estimated with the assumptions that the relationship between marked and total individuals found during the sampling period is the same for the whole population and that survival rate is constant and independent of age. In this study, only the adults and last nymphal stage were sampled. Jollys method considers only the most recent recaptures and the oldest are ignored (Begon 1979). This method calculates a survival rate for each sample (Begon 1979). Although the marks on the subadult stage could be lost, these individuals were also included in the population estimates because it is difficult to separate them from the adults in the field, and because this stage can span more than 9 months in some harvestmen species (Gnaspini 1996). The data obtained using each method were

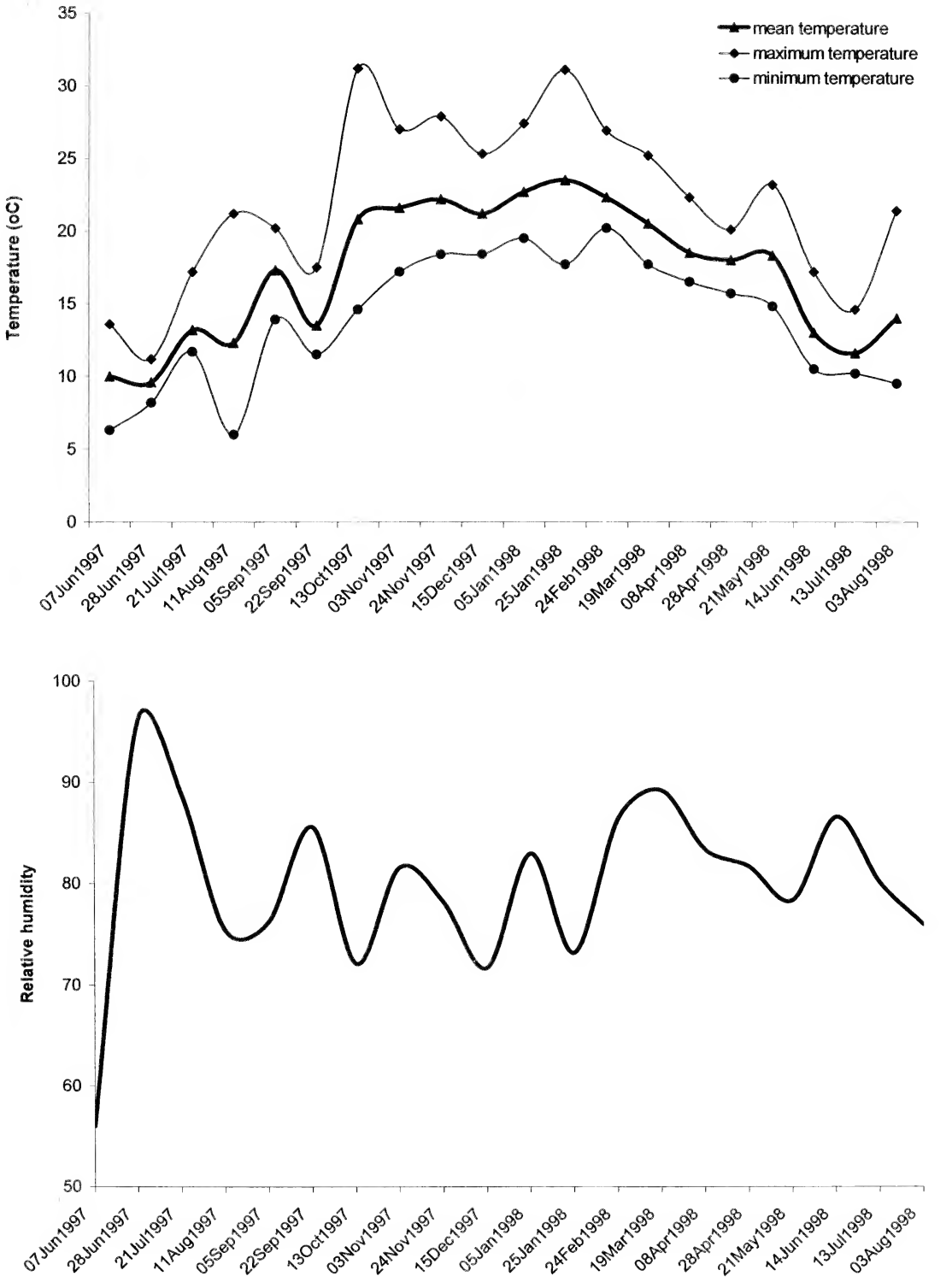


Figure 2.—Mean, maximum and minimum temperature (above) and relative humidity (below) in study site. Autumn began on 20 March, winter on 21 June, spring on 23 September and summer on 21 December.

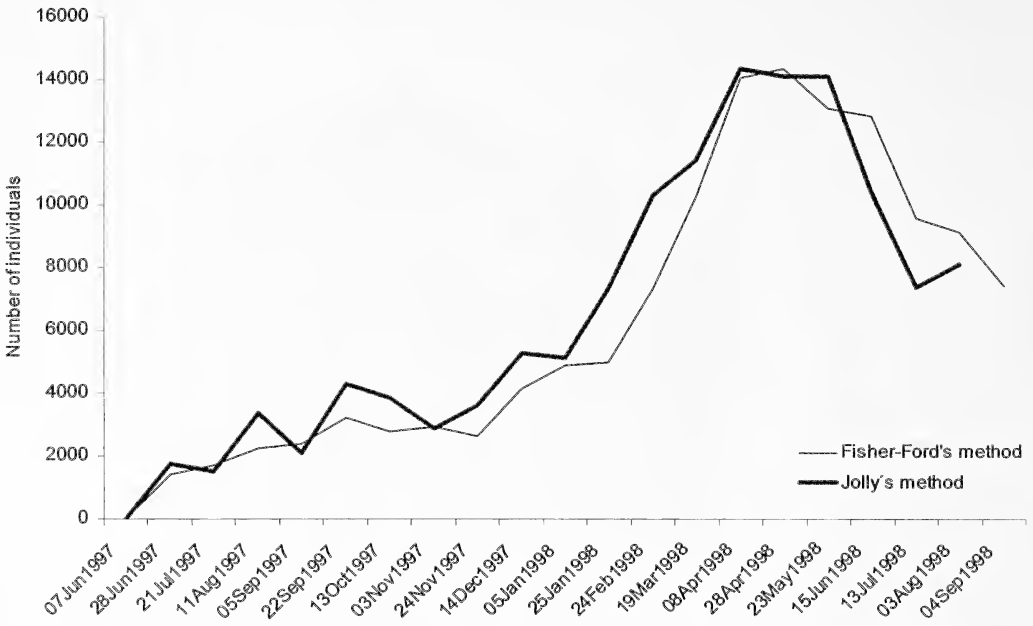


Figure 3.—Estimates of population size of adults and subadults of *Ilhaia cuspidata* by Jolly and Fisher Ford's capture-recapture methods in an Araucaria forest fragment in Brazil.

compared with a Mann-Whitney U test. Comparisons of population size between seasons were made with ANOVA and Tukey's $q$ test. The density of harvestmen at the study site was determined by dividing the population estimate divided by the total area of the fragment (30000 $m^2$). We used chi-square to test whether the sex ratio deviated from 1:1 and the association between juveniles and adults observed in the four seasons sampled. We used Kruskal-Wallis (KW) and Dunn's $Q$ to test for possible differences in harvestmen abundance in habitats with distinct concentrations of shelters, seasonal variations in abundance of other species of harvestmen, and seasonal differences in abundance of aggregations.

## RESULTS

**Population dynamics.**—The estimated population sizes of *Ilhaia cuspidata* were similar for both population estimation methods, Jolly and Fisher-Ford (Mann-Witney U = 178.00 $P = 0.624$) (Fig. 3, Appendix 1). The Fisher-Ford method presented less variation when compared with the Jolly estimate, probably due to the importance of all capture and recapture data points in the population size estimates. On the other hand, the Jolly method analyzed data more consistently for the day of captures/recaptures (Begon 1979). Herein, these data will be discussed mainly with the Fisher-Ford estimation method.

The population estimates ranged from a low of 1,429 individuals in the second sample (winter, 7 June, 1997), to a maximum of 14,445 in the sixteenth sample (autumn, 28 April, 1998). A slight and progressive population growth was observed from June to November of 1997, when the estimated values oscillated between 1,429 and 2,661 individuals (Fig. 4). There were significant seasonal differences in the mean population size of *Ilhaia cuspidata* showed a significant difference in winter and autumn, spring and autumn, and summer and autumn, (ANOVA $P < 0.0001$, Tukey $q = 16.3$ for winter vs autumn, 14.8 for spring vs autumn, 11.34 for summer vs autumn, $P < 0.001$). Population size remained low from the end of the winter (June) to the spring (November) and increased quickly in the following four months, during the spring and the summer (increasing 300%). In summer (January 1998) the population increased very rapidly, and in the period of four months, increased from 2,661 to 14,445 adult/subadult estimated individuals. The highest estimate occurred on the sixteenth sample date (28 April 1998), when 1,738 individuals were captured of which 1,227 were marked (Fig. 3,

Table 1.—Total number of males (M) and females (F) of harvestmen species observed on each sample date at the study site. *D.1. Discocyrtus* sp*1*, *D.2. Discocyrtus* sp*2*, *Tr. Tricommatidae*, *G.* sp. *Geraecormobius* sp., *I.c.* = *Ilhaia cuspidata* marked, jv. = juveniles, † = dead observed.

| Sample date | *D.1.* M | *D.1.* F | *D.2.* M | *D.2.* F | *Tr.* M + F | *G.* sp. M | *G.* sp. F | *I.c.* M | *I.c.* F | *I.c.* jv. | *I.c.*† |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 07 June 1997 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 157 | 135 | 8 | 0 |
| 28 June | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 113 | 73 | 1 | 0 |
| 21 July | 1 | 6 | 0 | 0 | 3 | 0 | 0 | 107 | 107 | 5 | 0 |
| 11 August | 0 | 2 | 1 | 0 | 4 | 1 | 1 | 131 | 131 | 2 | 0 |
| 05 September | 3 | 3 | 0 | 0 | 8 | 0 | 0 | 112 | 113 | 5 | 5 |
| 22 September | 4 | 6 | 1 | 1 | 8 | 2 | 0 | 127 | 159 | 0 | 1 |
| 13 October | 5 | 8 | 1 | 1 | 3 | 1 | 2 | 92 | 95 | 50 | 1 |
| 03 November | 8 | 13 | 1 | 1 | 4 | 2 | 2 | 78 | 134 | 144 | 1 |
| 24 November | 6 | 9 | 0 | 0 | 5 | 0 | 0 | 104 | 96 | 334 | 2 |
| 14 December | 4 | 5 | 1 | 1 | 6 | 1 | 0 | 149 | 136 | 226 | 1 |
| 05 January 1998 | 8 | 12 | 0 | 3 | 7 | 2 | 0 | 274 | 224 | 154 | 1 |
| 25 January | 16 | 11 | 0 | 0 | 4 | 4 | 5 | 300 | 267 | 141 | 3 |
| 24 February | 23 | 22 | 0 | 2 | 18 | 2 | 1 | 482 | 497 | 87 | 1 |
| 19 March | 13 | 18 | 1 | 2 | 6 | 1 | 1 | 539 | 624 | 94 | 8 |
| 08 April | 18 | 16 | 1 | 2 | 7 | 1 | 2 | 696 | 763 | 76 | 17 |
| 28 April | 5 | 9 | 3 | 2 | 11 | 0 | 0 | 567 | 660 | 38 | 20 |
| 23 May | 6 | 7 | 0 | 0 | 5 | 2 | 1 | 390 | 445 | 30 | 22 |
| 15 June | 3 | 10 | 1 | 2 | 8 | 0 | 1 | 324 | 374 | 23 | 34 |
| 13 July | 3 | 4 | 1 | 0 | 7 | 3 | 2 | 184 | 206 | 25 | 37 |
| 03 August | 4 | 8 | 0 | 0 | 13 | 2 | 2 | 151 | 159 | 24 | 34 |
| 04 September | 4 | 7 | 1 | 0 | 8 | 1 | 0 | 92 | 128 | 13 | 72 |
| Total | 136 | 178 | 13 | 17 | 136 | 26 | 20 | 5169 | 5526 | 1480 | 259 |

Appendix 1). The rates of recapture of marked individuals varied from 16% (28 June 1997) to 41% (24 November 1997) of the total captured in daylight.

The density of *Ilhaia cuspidata* in the study site varied between 0.05 adults/m$^2$ (in the winter) to 0.47 adults/m$^2$ (in the summer). The adult sex ratio was 1:1 for the entire study period ($X^2$ = 33.82 df = 20 $P < 0.027$). However, when the seasons were analyzed separately, only in spring the was sex ratio 1:1 ($X^2$ = 9.37 df = 3 $P < 0.024$), in other seasons these data showed alternating sex predominance (winter I: males > females $X^2$ = 5.13, df = 4, $P < 0.27$, summer: males > females $X^2$ = 6.99 df = 4 $P < 0.14$, autumn: males<females $X^2$= 9.28, df = 4, $P < 0.054$ and winter II: males < females $X^2$ = 3.049, df = 1, $P < 0.08$).

Immature individuals were observed in almost every sampling period. We counted 335 immatures during November 1997 (Table 1, Fig. 3), resulting in a maximum relative density of 0.01 immature/m$^2$. We observed significant association between the total number of juveniles and adults observed in each season ($X^2$ = 1566.2, 4 df, $P < 0.0001$), abundance of adults and juveniles are associated and there is probably a reproductive period. The higher number of juveniles observed in spring and summer was associated with the higher number of adults observed in summer and autumn (Table 1).

The differences in harvestman abundance in habitats with high (H), medium (M) and low (L) concentration of trunks and bricks is extremely significant (Trunks KW = 22.78, Dunn $Q_{L,H}$ = −22.4/$Q_{M,H}$ = −35.57 $P <$ 0.001; Bricks KW = 25.7, $Q_{L,H}$ = −32.12 / $Q_{l.M.}$ = −22.51 $P < 0.001$). These data show that, where there is higher concentration of trunks and/or bricks, there is a corresponding higher concentration of harvestmen. Stone and trash concentrations seem to be less important for concentrations of *Ilhaia cuspidata* (Stones KW = 10.07, Dunn $Q_{L,H}$ = −29,2 $P$ < 0.05; Trash KW = 12.88, Dunn $Q_{L,H}$ = −31.00/$Q_{L.M.}$ = −30.51 $P < 0.05$).

**Aggregations.**—We observed 522 aggregations of *Ilhaia cuspidata*, 6.5% with males only (*KS* = 0.24, mean per sample day X = 2; SD = 2.15; $n$ = 21); 9.2% females only

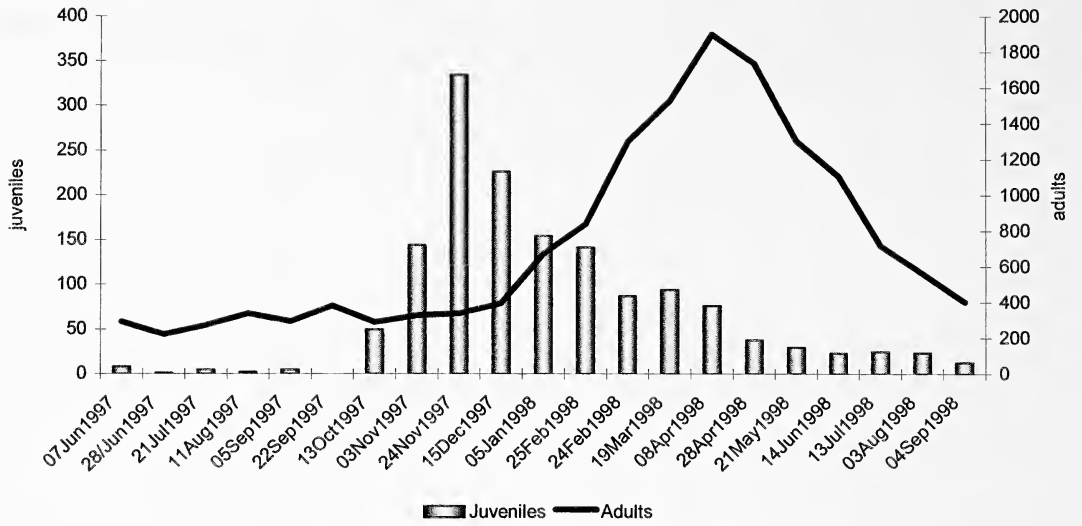


Figure 4.—Number of immatures and adults of *Ilhaia cuspidata* in an Araucaria forest fragment in Brazil.

(*KS* = 0.17; X = 2.7; SD= 2.13; *n* = 21); 56.9% males and females (*KS* = 0.18, X= 17.5; SD= 12.7; *n* = 21); 16.5% males, females and immatures (*KS* = 0.31 *P* = 0.02 NS); and 10.9% were multi-species aggregations (*KS* = 0.19, X= 3.3; SD= 2.66; *n* = 21) (Table 2).

Aggregations with fewer than five individuals were the most common kind of aggregations, but the number of these aggregations is constant through the year (KW = 10.176, $P = 0.03$, Dun's NS, $P > 0.05$). Aggregations that contained from 6–9 individuals show a significant increase in summer (Su) and autumn (Au) when compared with spring (Sp) (KW = 16.77, Dunn $Q_{SpSu} = -14.87$ $P < 0.01$, $Q_{SpAu} = -13.37$, $P < 0.05$). We also observed a significant increase in the number of aggregations with more those 10 individuals when comparing spring and autumn (KW = $15.00 Q_{SpAu} = -15.00$, $P < 0.05$). The analysis of all aggregations together shows similar results (KW = 14.72, $Q_{SpSu} = -13.62$, $Q_{SpAu} = -14.12$, $P < 0.05$). Thus, aggregations larger than six individuals were more abundant in summer and autumn.

**Individual movements and life span.**—During the three previous collections, taken before the sampling period, 238 individuals of *I. cuspidata* were individually marked (numbered). We recaptured 50 of those specimens during the 335 sample days. About 50% of these individuals were found in the same place that they were marked, 46% were found close to these sites (between 10 and 20 m) and the remained 4% were found approximately within 60 meters from the point that they were captured. These data show very low vagility of this opilionid species. The number of harvestmen recaptured decreased constantly across the study period and the last recaptures were made just one year after they had been marked, in the 15th sampling (April 1998). Longevity of adults is more than 455 days.

**Natural history.**—Field observations showed that *I. cuspidata* is practically motionless during the day, taking shelter in the interior or under fallen trunks, stones and pieces of wood. Individuals were also observed taking shelter under plastic objects and other trash. During the two nocturnal samples, one in the warm season (March 1998), and the other in the cold season (June 1998), we observed that the harvestmen began activity early in the night, about 15 minutes after sunset. An increase in the number of active individuals was observed 30 minutes after sunset, when it was almost dark (light intensity was 02 lux). On 15 June 1998, just after sunset, from 1730–1745 h, no active harvestmen were observed. The observations from 1750–1905 h revealed an incremental increase in harvestmen activity. From 1750–1805 h, all the individuals (16) of *I. cuspidata* seen were active; 18 were observed from 1810–1825 h; 38 from 1830–1845; and 44 from 1850–1905

Table 2.—Number of aggregations of *Ilhaia cuspidata* composed of only males (M); only females (F); males, females and juveniles (M + F + jv.); and interspecific aggregations (intrsp.).

| Date | M | F | M + F | M + F + jv. | Intrsp. | Total |
|---|---|---|---|---|---|---|
| 07 June 1997 | 4 | 6 | 19 | 1 | 1 | 31 |
| 28 June | 2 | 1 | 9 | 0 | 3 | 15 |
| 21 July | 2 | 3 | 15 | 0 | 1 | 21 |
| 11 August | 1 | 0 | 7 | 1 | 1 | 10 |
| 05 September | 3 | 4 | 17 | 0 | 4 | 28 |
| 22 September | 0 | 3 | 7 | 0 | 0 | 10 |
| 13 October | 0 | 1 | 9 | 2 | 4 | 16 |
| 03 November | 0 | 0 | 7 | 1 | 2 | 10 |
| 24 November | 0 | 0 | 3 | 1 | 1 | 5 |
| 15 December | 2 | 1 | 6 | 20 | 2 | 31 |
| 05 January 1998 | 2 | 3 | 12 | 10 | 5 | 32 |
| 25 January | 2 | 3 | 16 | 12 | 10 | 43 |
| 24 February 1998 | 9 | 5 | 36 | 12 | 8 | 70 |
| 19 March 1998 | 3 | 7 | 46 | 10 | 5 | 71 |
| 08 April 1998 | 2 | 5 | 37 | 12 | 3 | 59 |
| 28 April 1998 | 1 | 2 | 31 | 3 | 5 | 42 |
| 21 May 1998 | 1 | 3 | 20 | 2 | 2 | 28 |
| Total | 34 | 47 | 297 | 87 | 57 | 522 |
| % | 6.50 | 9.20 | 56.90 | 16.50 | 10.90 | 100.00 |

h. Activity during daylight was never observed outside the shelters.

In the field, individuals of *I. cuspidata* were observed feeding on small adult lepidopterans, bird and rodental feces (probably Cricetidae). In captivity, individuals accepted several kinds of vegetables and fruits (e.g. papaya, banana, peach, beet, and carrot).

We observed animals coexisting with *I. cuspidata*, such as toads, worms (Oligochaeta and Hirudinea), crickets, spiders, pulmonate mollusks, pseudoscorpions, coleopterans (Passalidae, Staphylinidae) and other insects. Frequently, we observed the presence of small crickets (Phalangopsidae) and a species of pulmonate mollusk near *I. cuspidata*.

The spider *Scytodes* sp. (Araneae, Scytodidae), was observed preying on a young *I. cuspidata*, and feeding on the remains of an adult exoskeleton. One dead individual of *I. cuspidata* was found in the web of a Theridiidae spider. Besides these predators, it is possible that toads (*Bufo* sp.), ants (*Pachycondyla* sp. and *Odontomachus* sp.) and some spiders (e.g. *Ctenus* sp.) in the study site could prey on harvestmen.

Egg-batches of *I. cuspidata* were rarely found (even previous to the peak of young recruitment), probably due to the difficulty of locating them among the leaf litter. The eggs measured approximately 1mm in diameter, were white in color, opaque and sticky. They were laid under fallen leaves in clusters of up to 20 and did not receive any additional care by the female. An egg batch containing 8 eggs was collected in the field and maintained in a plastic box with leaves and wet cotton in the bottom. After 3 weeks, four nymphs hatched.

**Other harvestmen species.**—Other harvestmen species observed coexisting with *Ilhaia cuspidata* were two species of *Discocyrtus* (Gonyleptidae, Pachylinae, one black, sp.1 and another red, sp.2), one species of *Geraecormobius* sp. (Gonyleptidae, Gonyleptinae), and one species of an unidentified genus of Tricommatidae. We observed significantly higher abundance of *Discocyrtus* sp.1 in summer (Su) and autumn (Au) when compared with the first winter studied (Wi) (KW = 13.93, $P = 0.007$; $Q_{WiSu} = -12.4$, $Q_{WiAu} = -13.2$, $P < 0.05$). We also observed an increase in Tricommatidae (24 February 1998), *Geraecormobius* sp. (25 January 1998) and *Discocyrtus* sp.2 (28 April 1998) (Fig. 5 & Table 1). These species seem to have a population increase in the same season as *Ilhaia cuspidata* and *Discocyrtus* sp.1, however there is

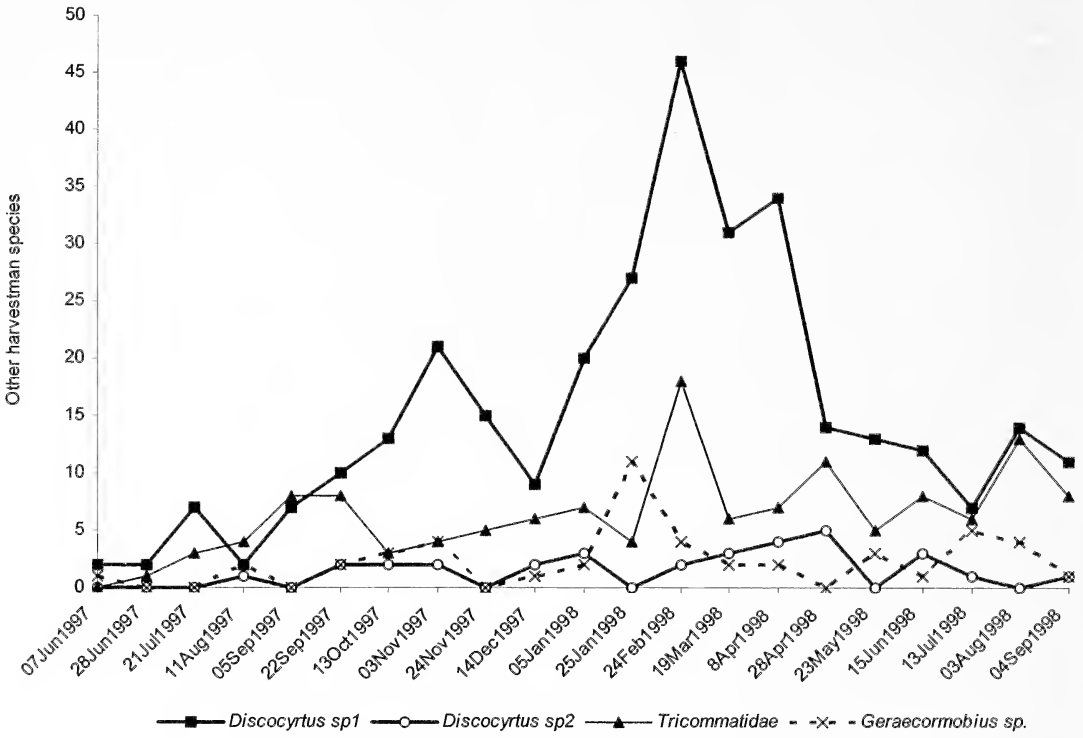


Figure 5.—Total number of four species of opilionids (adults and immatures) observed in an Araucaria forest fragment in Brazil.

insufficient data to strongly support this observation.

## DISCUSSION

Biological activities of populations, mainly in tropical regions, can be linked to seasonal parameters such as temperature and rainfall (Opler et al. 1976; Winemiller 1989; Machado & Oliveira 1998). The harvestman *Cynortoides cubanus* Banks 1909 (Cosmetidae) decrease post-embryonic development at higher temperatures (Juberthie 1972). In the same way, there could be a specific temperature that favors *Ilhaia cuspidata* juveniles to survive in higher numbers until the adult stage. Our data show that the high number of juveniles observed in spring and summer was associated with the high number of adults observed in summer and autumn, suggesting that there is a definite period of successful reproduction, with a subsequent adult population increase.

The constant presence of juveniles during the whole year, suggests a continuous reproduction with a peak of emergence just after winter or, delayed hatching. Young and adults often are under different selection pressures, and reproductive effort reflects the environmental factors that put pressure on the adults as well as on the juveniles (Pianka 1994). In this respect, a species with high mortality needs a corresponding high fecundity, persisting despite the great decline of the population (Pianka 1994). Very low temperatures should eliminate a great part of the population, mainly the juveniles. However, there could be a possible decrease in activity and/or movement to other shelters (under soil surface or fallen leaves, available all year) during the coldest times, resulting sub- or super-estimation in certain seasons.

In contrast to the cavernicolous harvestmen, such as *Goniosoma spelaeum* (studied by Gnaspini 1996), *Pachylospeleus strinatii* (studied by Pinto-da-Rocha 1996a), and *Daguerreia inermis* (studied by Pinto-da-Rocha 1996b), the epigean *I. cuspidata* had great seasonal variation in population size. In caves the temperature is less variable than epigean habitats (Culver 1982) and probably the seasonal temperature variation observed in the *Araucaria* forest influences this population. The al-

ternating sex ratio of the seasons could reflect these fluctuations.

The significant difference in harvestmen abundance in habitats with varying concentrations of trunks and bricks indicates that these shelter preferences can be linked to microhabitat conditions promoted by these materials. Wood and clay provide shelters with less temperature variation than stones and plastic objects. The great abundance of this harvestmen species in this study site could be linked to their adaptation or preference for these abundant shelters.

Capocasale & Bruno-Trezza (1964) observed that behavior of harvestmen was related to changes in the temperature. They demonstrated that the number of aggregated individuals of *Acanthopachylus aculeatus* (Kirby 1818) (Gonyleptidae) was inversely proportional to the temperature, with the largest aggregations occurring in lower temperatures. We observed that *I. cuspidata* increase in number of larger aggregations during the summer and autumn compared with the spring, thus the number of aggregated individuals was not increasing with lower temperatures. So, results suggest that the increase of aggregated individuals is not influenced by temperature, but probably by the population density. Aggregation occurs at the limited number of favorable shelter sites(with no light and high moisture, like bricks).

In contrast to *Goniossoma longipes* (Machado & Oliveira 1998) and *Goniosoma proximum* (Ramirez & Giaretta 1994), which guard their egg batches (60–210 eggs) or juveniles, parental care of the low number of egg batches (approximately 20 eggs) was not observed for *Ilhaia cuspidata*. We can not say if *I. cuspidata* only lays about 20 eggs during the entire reproductive period or lays several egg batches in different shelters as a way to avoid predation.

An increase in active individuals at dusk demonstrates that *I. cuspidata* is nocturnal, forages near shelters, and are restricted to small areas (around 50 $m^2$). This observation supports the concept of a small home range for gonyleptideans, as was also observed for *Goniosoma spelaeum*, *Daguerreia inermis* and *Pachylospeleus strinatii* (Gnaspini 1996; Pinto-da-Rocha 1996a, 1996b).

These harvestmen have a very broad diet, as was also observed for *Acanthopachylus aculeatus* (Capocasale & Bruno-Trezza 1964), *Pachyloidellus goliath* (Acosta 1995), *Pachylospeleus strinatii* (Pinto-da-Rocha 1996) and *Goniosoma spelaeum* (Gnaspini 1996), *G. longipes* (Machado & Oliveira 1998), and *Daguerreia inermis* (Pinto-da-Rocha 1996b). Besides small live animals and plants, we observed this species feeding on the feces of birds and rats, an observation also documented by Hillyard & Sankey (1989) for another species, thus reaffirming an omnivorous diet for harvestmen.

The *I. cuspidata* population in this study experienced high fluctuations in the number of individuals, a probable delayed response to climate fluctuations. These population fluctuations were also observed for other harvestmen species in the study site, and possibly these harvestmen have similar responses to these environmental conditions.

## ACKNOWLEDGMENTS

We are grateful to Anderson K. Fujioka, Antonio Serbena, Luís Coltro Jr. and Renata C. C. Sousa for help with fieldwork, and to Glauco Machado for suggestions on the manuscript. We thank José Roberto Varani for help with statistical analyses. We are grateful to the director of the "Museu de História Natural Capão da Imbuia" for permitting access to the study site and to Pedro Gnaspini who kindly permitted the use of his computer mark-recapture program.

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Appendix 1.—Number of captured (CAP), released (REL) and recaptured (D1 = day, D2 = 22, second day of recapture, D3 = 45, third day of recaptures . . .) adults and subadults of *Ilhaia cuspidata* in Curitiba, Paraná, Brazil.

| | | | Recaptures | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Day | CAP | REL | D1 | D2 | D3 | D4 | D5 | D6 | D7 | D8 | D9 |
| 1 | 292 | 292 | | | | | | | | | |
| 22 | 222 | 222 | 36 | | | | | | | | |
| 45 | 272 | 272 | 23 | 35 | | | | | | | |
| 66 | 338 | 338 | 24 | 16 | 36 | | | | | | |
| 91 | 297 | 295 | 17 | 9 | 26 | 30 | | | | | |
| 108 | 380 | 380 | 8 | 10 | 17 | 19 | 40 | | | | |
| 129 | 298 | 290 | 6 | 7 | 12 | 15 | 30 | 33 | | | |
| 150 | 332 | 327 | 6 | 4 | 11 | 17 | 22 | 28 | 27 | | |
| 171 | 339 | 339 | 7 | 7 | 13 | 13 | 18 | 26 | 15 | 40 | |
| 191 | 396 | 395 | 2 | 5 | 9 | 3 | 13 | 9 | 12 | 31 | 26 |
| 213 | 671 | 670 | 3 | 2 | 9 | 8 | 16 | 10 | 13 | 23 | 20 |
| 232 | 850 | 838 | 5 | 0 | 7 | 2 | 9 | 14 | 10 | 24 | 22 |
| 263 | 1314 | 1297 | 4 | 4 | 6 | 6 | 12 | 11 | 9 | 22 | 21 |
| 286 | 1526 | 1526 | 4 | 4 | 6 | 7 | 9 | 6 | 8 | 19 | 18 |
| 306 | 1896 | 1896 | 2 | 2 | 7 | 4 | 8 | 5 | 9 | 11 | 9 |
| 326 | 1738 | 1736 | 4 | 2 | 8 | 7 | 5 | 13 | 3 | 6 | 11 |
| 349 | 1304 | 1304 | 5 | 3 | 3 | 4 | 7 | 8 | 6 | 4 | 6 |
| 373 | 1105 | 1105 | 4 | 1 | 6 | 3 | 6 | 6 | 1 | 6 | 5 |
| 402 | 715 | 714 | 1 | 0 | 2 | 2 | 2 | 2 | 4 | 4 | 3 |
| 423 | 562 | 562 | 0 | 0 | 2 | 0 | 1 | 2 | 2 | 3 | 3 |
| 455 | 403 | 403 | 2 | 1 | 0 | 0 | 1 | 1 | 3 | 2 | 2 |

Appendix 1.—Extended.

| Recaptures | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| D10 | D11 | D12 | D13 | D14 | D15 | D16 | D17 | D18 | D19 | D20 |
| 68 | | | | | | | | | | |
| 35 | 143 | | | | | | | | | |
| 31 | 89 | 103 | | | | | | | | |
| 22 | 42 | 68 | 150 | | | | | | | |
| 3 | 30 | 50 | 108 | 189 | | | | | | |
| 7 | 21 | 24 | 57 | 114 | 227 | | | | | |
| 3 | 17 | 22 | 37 | 59 | 120 | 165 | | | | |
| 4 | 7 | 8 | 32 | 41 | 83 | 92 | 102 | | | |
| 4 | 8 | 9 | 15 | 32 | 44 | 64 | 52 | 77 | | |
| 2 | 2 | 4 | 10 | 27 | 27 | 37 | 30 | 50 | 50 | |
| 1 | 5 | 4 | 3 | 18 | 16 | 22 | 15 | 33 | 28 | 26 |

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# PHENOLOGY OF LINYPHIIDS IN AN OLD-GROWTH DECIDUOUS FOREST IN CENTRAL ALBERTA, CANADA

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**ABSTRACT.** Spiders in the family Linyphiidae are numerically dominant and show remarkably high diversity in northern forests, but relatively little is known about their phenology in northern latitudes of North America. We report a phenological summary of close to 6,000 individual linyphiids representing 17 species. These were collected by pitfall trapping during two snow-free seasons in an old-growth deciduous boreal forest in central Alberta, Canada. Three species of approximately the same body size, *Allomengea dentisetis* (Grübe 1861), *Bathyphantes pallidus* (Banks 1892), and *Lepthyphantes intricatus* (Emerton 1911), dominated the sample, and showed three distinct patterns of peak activity. This suggests temporal stratification as a possible mechanism that explains their co-existence. Four less commonly collected species within the same genus (*Walckenaeria*) showed similar seasonal segregation in periods of peak activity. Comparisons with other literature suggest the general phenology of many linyphiids is conserved across continental and global scales.

**Keywords:** Species co-existence, life-history, boreal forest, pitfall trapping

The family Linyphiidae (sensu lato) is the second most diverse spider family globally (Coddington & Levi 1991), and is notable in attaining greatest diversity in north temperate latitudes rather than towards the equator. As such, linyphiids dominate northern spider faunas (Helsdingen 1983). A notable biological feature associated with this high northern diversity is a flexibility of phenology (seasonal sequence of life history events) among members of the family. Linyphiid species display most of the phenological patterns known among spiders: multivoltine and univoltine strategies predominate in warmer climates, and the reproductive period of univoltines may occur in various seasons and for varying durations (Merrett 1969; Berry 1971; Draney 1997a, b; Draney & Crossley 1999). Northward, biennial and mixed annual-biennial strategies (in which some members of a population are annual and some are biennial) become more common (Schaefer 1977; Toft 1976, 1978). Different species overwinter as juveniles, adults, or (more rarely), eggs (Schaefer 1976, 1977), and some species actively feed and even reproduce during the northern winter (Huhta & Viramo 1979; Aitchison 1978, 1984).

Phenological flexibility has also been documented within linyphiid species, with longer cycles being displayed by more poleward populations (Almquist 1969; Toft 1976). Besides being a response to climate, phenological patterns are also associated with other ecological factors including vertical stratification of the spider (Toft 1978) and habitat type (Draney & Crossley 1999). Certainly, within any climatic regime, a variety of phenological patterns may be displayed by different linyphiid species.

Most of the work on linyphiid phenology has examined western and northern European populations experiencing relatively mild maritime-influenced climates (Juberthie 1954; Tretzel 1954; Almquist 1969; Merrett 1969; Toft 1976, 1978; De Keer & Maelfait 1987, 1988; Hauge 2000). With the exception of work in Finland (e.g., Huhta 1965, 1971; Palmgren 1972; Niemelä et al. 1994), less is known about linyphiid phenological responses to harsher continental boreal climates, such as

our study site in central Alberta, where seasonal variation is extreme. Some work has been done on the subnivean winter activity of spiders in these continental climates (Aitchison 1978, 1984). The present work examines growing season phenology of linyphiids in a sub-boreal climax deciduous forest. Our objectives include describing the phenological patterns of the common linyphiids as well as attempting to identify factors that might explain the variation in phenological patterns among the species in this system. We acknowledge that conclusions about phenology may be limited to our study location, sample period, and study years, but nonetheless hope to increase knowledge about a poorly understood component of the boreal spider fauna.

## METHODS

**Study site.**—The study forest is located at the George Lake Field Station, located 75 km northwest of Edmonton, Alberta, Canada (53°57′N, 114°06′W). This old-growth deciduous forest has been left relatively undisturbed for over 100 years. The work described here was part of two larger projects investigating the relationship between ground-dwelling spiders and fallen logs, or downed woody material (Buddle 2001 a, b). The first project occupied an area of approximately 2.5 ha at the northeast section of the field station. The second project comprised about 3.5 ha in the northwest portion of the forest. Both projects were conducted in homogenous regions of this boreal mixed-wood forest, which is dominated by two *Populus* species: trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.). Less common tree species in the area include birches (*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)), white spruce (*Picea glauca* (Moench)) and black spruce (*P. mariana* (Mill.) BSP). Further vegetation details can be found in Niemelä et al. (1992).

**Sampling and spider identifications.**—Ground-dwelling spiders were sampled with 88 pitfall traps in 1998 and 232 pitfall traps in 1999. All 88 traps in 1998, and 88 of the pitfall traps in 1999 were white circular (11 cm diameter) plastic containers sunk into the ground with the lip flush to the substrate surface (Spence & Niemelä 1994); 2–3 cm of preservative was used in the traps (silicate-free ethylene glycol) and a plywood roof measuring 15 × 15 cm was elevated 2–3 cm above the traps to prevent flooding and trap disturbance. The additional 144 pitfall traps used in 1999 were smaller (6 cm diameter), made of clear plastic, and were covered with a circular plastic roof (11 cm diameter). Larger traps were placed 10–15 m apart; smaller pitfall traps were all 2 m from an adjacent trap (see Buddle (2001 a, b) for complete details regarding sampling design).

There has been some debate over the use of pitfall traps to sample ground-dwelling arthropods, as such traps are biased by the activity of the organism, and are influenced by such factors as trap material, type of preservative and color (e.g., Luff 1975; Adis 1979; Curtis 1980; Merrett & Snazell 1983; Topping 1993). However, pitfall traps have been shown to efficiently sample ground-dwelling spiders (e.g., Uetz & Unzicker 1976; Draney 1997 a, b; Buddle et al. 2000), and provided that no statements are made about absolute density, pitfall traps can be used to quantitatively assess periods of peak activities of male and female spiders (Toft 1976, 1978; De Keer & Maelfait 1987; Draney & Crossley 1999).

Sampling was continuous over the snow-free season in both years; in 1998 pitfall traps were placed in the forest on 4 May and removed on 10 September. Pitfall traps were opened from 20 April until 24 September in 1999. This provided 126 days of continual pitfall trapping in 1998 and 154 continuous trapping days in 1999. There were eight collection times (approximately every 15–20 days) in each year.

Samples were sorted and stored in 70% ethanol. All adult spiders were identified to species with nomenclature following Platnick (2003), and Buckle et al. (2001) for linyphiids. Voucher specimens of all taxa have been deposited in the Strickland Entomological Museum (Department of Biological Sciences, University of Alberta) and the Northern Forestry Centre Arthropod Collection, both in Edmonton, Alberta, Canada.

**Data standardization and analysis.**—Increasing sampling effort (i.e., number of traps) corresponds to an increase in the total catch of individuals (Niemelä et al. 1986). It was therefore necessary to standardize the collection data from 1998 and 1999 to account for variation in trapping effort. Without this standardization, it would be difficult to separate

true differences in relative abundance from simply differences in sampling effort. Prior to data standardization, however, species by sample accumulation curves were constructed using EstimateS Version 6.0 (Colwell 1997). This was to ensure that linyphiid species richness from 1998 (88 pitfall traps) and 1999 (232 traps) had leveled off, and thus represented complete samples. Only in this case would further standardization be justified. When this criterion was met, and when collections from different years were compared, pitfall trap data were adjusted to make catch data relative to a predetermined number of pitfall traps; since there were 88 traps in 1998 and 232 traps in 1999, data for both years were standardized to catches per 160 traps (average number of traps per year). Samples in 1998 were multiplied by 1.82 (i.e., 160/88), and samples in 1999 were multiplied by 0.69 (i.e., 160/232). Data were not standardized to account for differences in pitfall trap size (i.e., 6 cm versus 11 cm diameter) as Work et al. (2002) show catches of spiders do not vary significantly between these trap sizes.

Linyphiid species represented by fewer than 15 individuals in the collection were excluded prior to analyses as these would be too few to adequately assess phenological patterns. It was assumed that periods of peak male and female activity correspond to the peak reproductive period for the species (e.g., De Keer & Maelfait 1987; Draney 1997 a, b). Graphical analysis was used to assess this reproductive period and to evaluate the year-to-year variation in catches of the common ground-dwelling spiders. Results were compared to other published records and to information available on the same or closely related species from different geographic regions. Additionally, we measured the carapace width (CW) of our study spiders to ascertain overall spider size (Hagstrum 1971) to determine if any phenological patterns differed by species size. For these measures, a sub-set (i.e., 3–5 individuals) of both males and females were measured under a dissecting microscope fitted with an ocular micrometer. These measures were used purely in a relative sense, and thus sample sizes were small, and measures of variance were not used.

## RESULTS

A total of 5,944 individuals representing 50 species of linyphiids were collected. Linyphiids represented 32% of the total number of spiders collected experiment-wide, and 46% of the total number of species collected (see Buddle 2001a for complete species list). Of the linyphiids, 17 species were represented by $\geq$ 15 individuals, and these accounted for $>$ 98% of the total number of linyphiids collected (Table 1). Three species accounted for most of the linyphiids (87.2% of the total linyphiids collected): *Allomengea dentisetis* (Grübe 1861), *Bathyphantes pallidus* (Banks 1892), and *Lepthyphantes intricatus* (Emerton 1911) (Table 1).

Species accumulation curves show that the observed species richness of the linyphiids had leveled off at about 80 samples in 1998 and about 65 samples in 1999 (Fig. 1). This illustrates that we adequately sampled linyphiids in this study, and comparisons across years are justified, as is standardization to account for sampling effort.

On a per-trap basis, about the same number of linyphiids were collected in 1998 (mean ($\pm$ SE) of 21.53 $\pm$ 1.39 spiders per trap, $n$ = 88)) as in 1999 (17.02 $\pm$ 0.57, $n$ = 232). Standardized to 160 traps, we collected 3445.5 linyphiids in 1998 and 2722.8 in 1999. When the total male and female catch of the 17 linyphiid species is plotted by year and sampling time, it is apparent that males were more common in pitfall traps than were females. The peaks in female activity generally corresponded with the peak in male activity (Fig. 2). In both years female linyphiids were most commonly collected late in the season; males were more common in pitfall traps late in the season in 1998, but were less variable across collection dates in 1999 (Fig. 2).

Collections of the three common linyphiids showed three different phenological patterns, and these patterns were similar for both collection years (Fig. 3). *Allomengea dentisetis* was most active in August and September, *B. pallidus* in late July–August, *L. intricatus* in June. In general, females were less frequently collected than males, but their peak in activity corresponded closely to male activity (Fig. 3).

When the phenologies of all 17 linyphiid species are depicted, it is clear that periods of peak activity vary both in when males and females occur, and in the length of time both males and females are active (Fig. 4). For example, males and females of *L. intricatus*, *B. pallidus*, and *Microneta viaria* (Blackwall

Table 1.—Mean carapace width (CW, mm), number of females, and number of males, for 17 species of Linyphiidae collected by pitfall traps in 1998 and 1999, in a deciduous forest in north-central Alberta. Species arranged by size (descending).

| Species | CW | Females | Males | Total |
|---|---|---|---|---|
| *Pityohyphantes costatus* (Hentz 1850) | 2.80 | 19 | 20 | 39 |
| *Allomengea dentisetis* (Grübe 1861) | 1.36 | 1068 | 1719 | 2787 |
| *Neriene clathrata* (Sundevall 1830) | 1.28 | 2 | 30 | 32 |
| *Helophora insignis* (Blackwall 1841) | 1.20 | 41 | 30 | 71 |
| *Lepthyphantes intricatus* (Emerton 1911) | 1.14 | 124 | 532 | 656 |
| *Oreonetides vaginatus* (Thorell 1872) | 1.13 | 13 | 60 | 73 |
| *Centromerus sylvaticus* (Blackwall 1841) | 1.02 | 1 | 14 | 15 |
| *Bathyphantes pallidus* (Banks 1892) | 0.88 | 433 | 1311 | 1744 |
| *Walckenaeria prominens* Millidge 1983 | 0.82 | 3 | 64 | 67 |
| *Walckenaeria castanea* (Emerton 1882) | 0.81 | 26 | 0 | 26 |
| *Microneta viaria* (Blackwall 1841) | 0.78 | 12 | 130 | 142 |
| *Lepthyphantes zebra* (Emerton 1882) | 0.78 | 2 | 30 | 32 |
| *Walckenaeria directa* (O. P.-Cambridge 1874) | 0.77 | 5 | 34 | 39 |
| *Sciastes truncatus* (Emerton 1882) | 0.66 | 0 | 36 | 36 |
| *Walckenaeria atrotibialis* (O. P.-Cambridge 1878) | 0.66 | 0 | 25 | 25 |
| *Pocadicnemis americana* Millidge 1976 | 0.56 | 0 | 21 | 21 |
| *Diplocentria bidentata* (Emerton 1882) | 0.53 | 2 | 36 | 38 |
| Total | | 1751 | 4092 | 5843 |

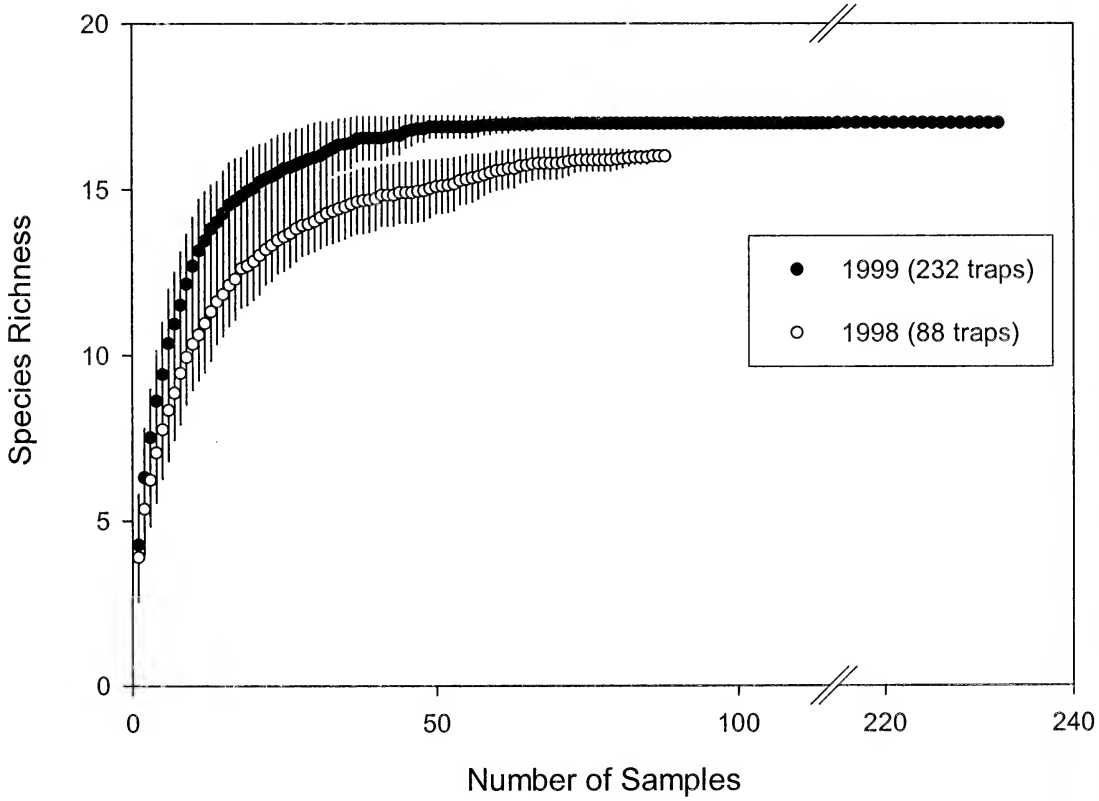


Figure 1.—Observed species accumulation curve of species richness by samples (pitfall traps) in 1998 (88 traps) and 1999 (232 traps). Data were re-sampled (randomly, without replacement) 50 times, error bars are ± 1 SD.

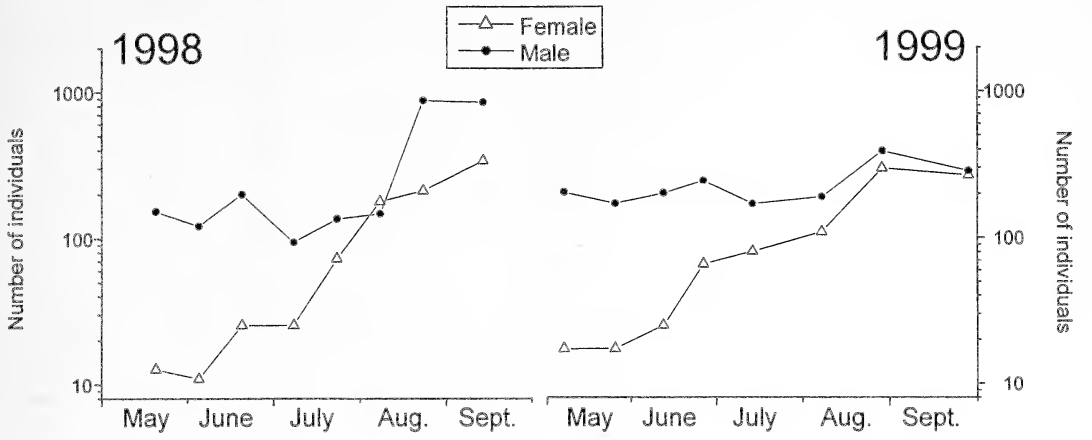


Figure 2.—Total number of male and female linyphiids (17 species) collected by pitfall traps in an old-growth deciduous forest. Note log-scale on axis. Number of individuals standardized to 160 pitfall traps.

1841) were caught in pitfall traps for much of the collection period, whereas many of the smallest linyphiid species collected show reduced periods of activity early in the season (e.g., *Diplocentria bidentata* (Emerton 1882), *Walckenaeria directa* (O.P.-Cambridge 1874) and *Lepthyphantes zebra* (Emerton 1882)) (Fig. 4). Smaller-bodied linyphiids were seldom collected past mid-summer whereas some of the larger-bodied species show higher catches in pitfall traps late in the season (e.g., *A. dentisetis*, *Helophora insignis* (Blackwall 1841) and *Centromerus sylvaticus* (Blackwall 1841)) (Fig. 4). Species within the same genus also show some differences in periods of peak activity. For example, collections of the four *Walckenaeria* species never overlap in time, and *L. zebra* occurs early in the season whereas *L. intricatus* shows a peak in activity about 3 weeks later (Fig. 4). It should be noted, however, that many of the species depicted in Fig. 4 were relatively rare in the collection (Table 1), so statements about their phenology should be interpreted with caution.

## DISCUSSION

Linyphiids are dominant on the forest-floor in our old-growth study forest, in terms of both diversity and relative abundance; they represented almost half the total species collected and one third of the number of individuals collected. Our work represents one of the few detailed accounts of linyphiid phenology from northern regions of North America. We have presented data that shows three species, of approximately the same relative body size, are remarkably common on the forest floor of north-central Alberta: *A. dentisetis*, *L. intricatus*, and *B. pallidus*. These species have also been shown to dominate the fauna of boreal-mixed wood forests throughout north-central Alberta (Buddle et al. 2000; Buddle 2001a). An important question is how these linyphiids might coexist on the forest floor, and the phenological summary may provide some clues.

It has long been suggested that seasonal segregation of similar-sized spiders might promote species co-existence (e.g., Breymeyer 1966; Williams 1962; Uetz 1977). In our work *A. dentisetis* shows a period of peak activity late in the season (August–September), *L. intricatus* early in the season (June), and *B. pallidus* in mid-summer. Thus, temporal segregation may be the mechanism that promotes co-existence of these linyphiids in northern boreal forests. We also see this general pattern within the genus *Walckenaeria* and *Lepthyphantes* from our collections. Future work will have to test this hypothesis, and it is difficult to claim generality from our limited collection time, and limited study area.

There are clearly other linyphiids that also co-occur with *A. dentisetis*, *B. pallidus*, and *L. intricatus*, but these may not directly interact with the three dominant species as they are either relatively rare in our collections, or are of a smaller body size (e.g., *Walkenaeria* species, *M. viaria*) (Table 1; Fig. 4), or they use herbaceous vegetation as additional foraging sites. For example, *H. insignis* is commonly collected by sweeping the vegetation in boreal

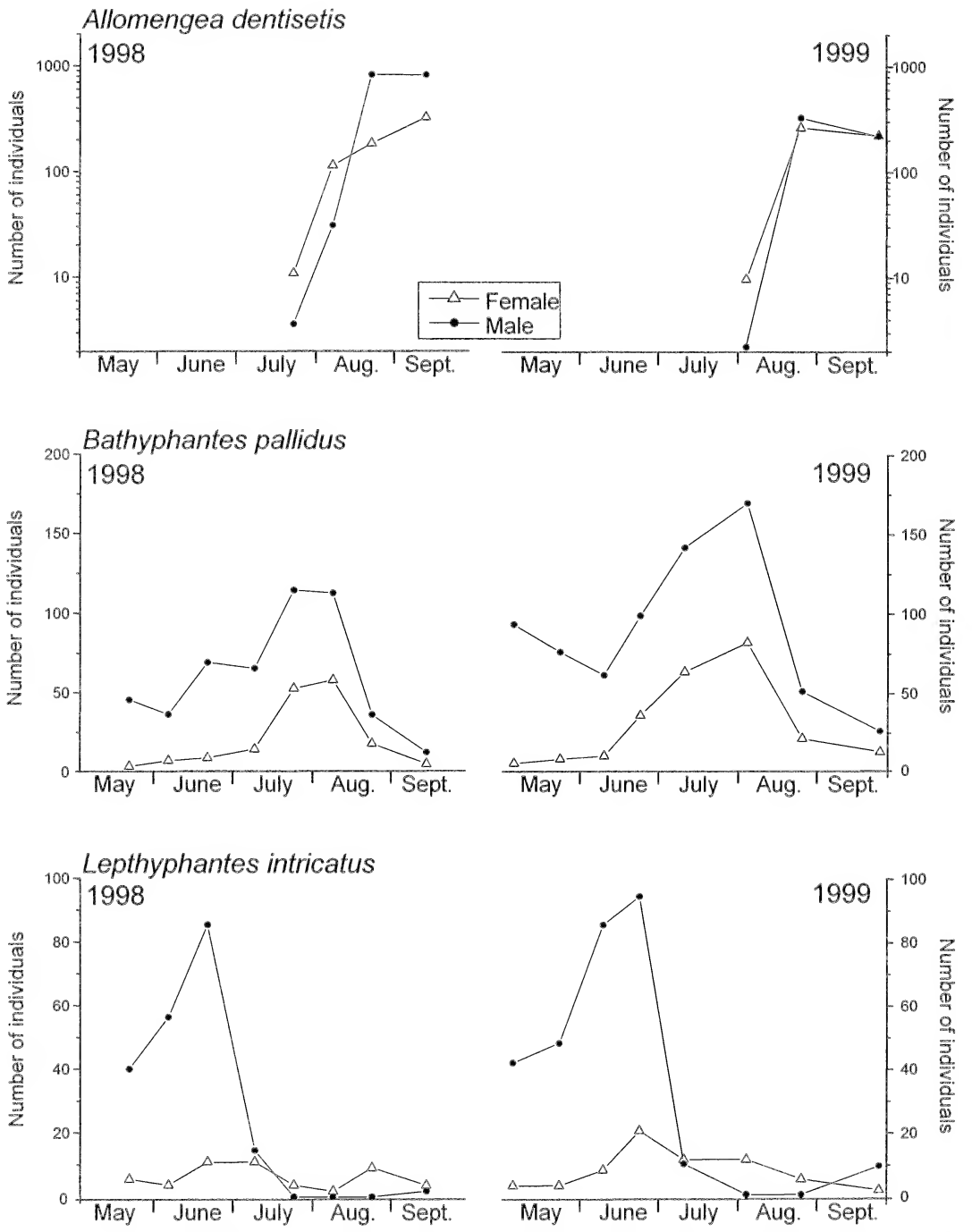


Figure 3.—Total number of male and female *Allomengea dentisetis* (top), *Bathyphantes pallidus* (middle), and *Lepthyphantes intricatus* (bottom) collected by pitfall traps in an old-growth deciduous forest. Note log-scale on axis of top graph. Number of individuals standardized to 160 pitfall traps.

mixed-wood forests (Buddle et al. 2000), and *H. insignis* and *Pityohyphantes costatus* (Hentz 1850) have often been observed in webs located in the herbaceous vegetation at our study forest (C.M. Buddle, pers. obs.). These species do use the forest floor as evident from our pitfall trap collections, but their main foraging location may be in the herba-

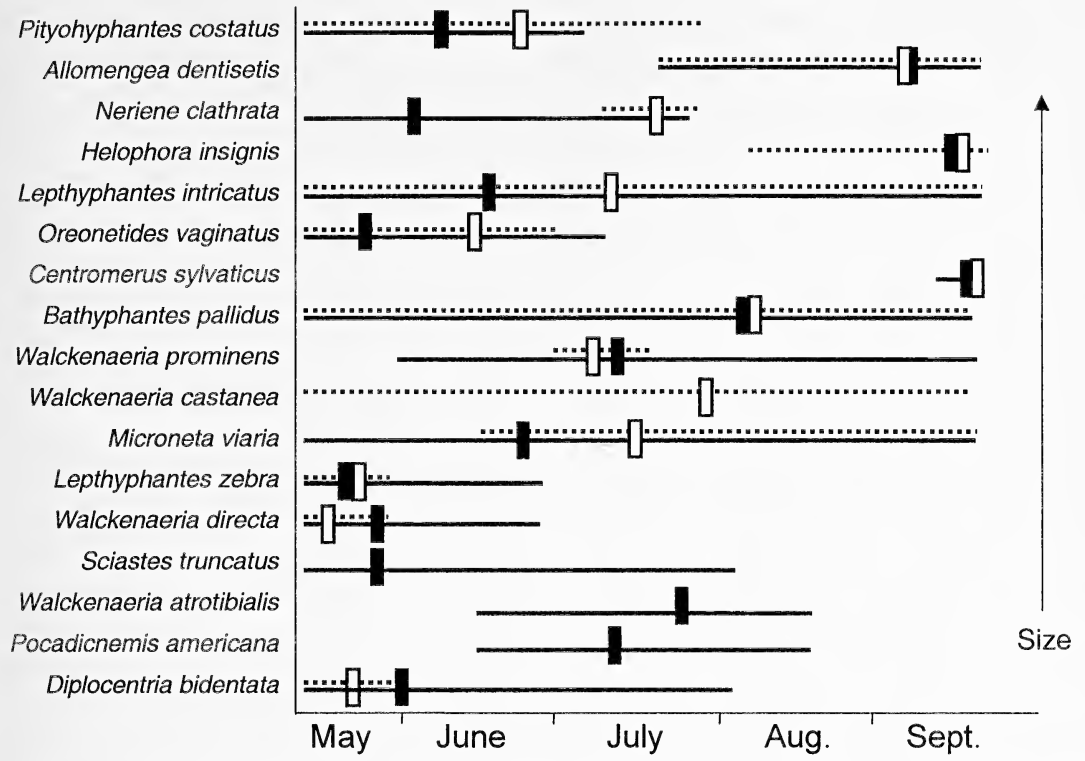


Figure 4.—Phenological summary of 17 linyphiid species collected over two years (pooled). Horizontal line indicates continuous periods when males (solid) and females (dashed) were collected. Vertical blocks represent peak activity of males (solid) and females (open), represented by weighted average of males or females collected by sampling period. Species size (smallest to largest, moving vertically) was determined by averaging carapace width for males and females.

ceous layer. Therefore, other larger-bodied species may interact with the three dominant species, but the frequency of interactions may be relatively low due to vertical habitat stratification (e.g., Turnbull 1960; Luczak 1966).

We can compare our phenological summaries with other published accounts of seasonal activity of linyphiids to determine whether any species or genera show consistent patterns across larger scales. We focus first on research by Niemelä et al. (1994) in Finland, as this work was also done in a mature forest in a climate with similar seasonal extremes as found in northern Alberta. Additionally, Niemelä et al. (1994) rely on pitfall trap data to ascertain peaks in spider activity, making comparisons with our study relevant, and several of the same species and genera are common to both studies.

Many of our results confirm research by Niemelä et al. (1994): *D. bidentata* occurs most commonly in early season, *M. viaria* is most frequently collected from June–early August, *Oreonetides vaginatus* (Thorell 1872) is most abundant early in the season, and *H. insignis* does not appear in collections until August. Therefore, the seasonal occurrence of some linyphiids is conserved, even on different continents.

*Centromerus sylvaticus* is known to be active in the winter under the snow layer in central Canada (Aitchison 1978). The entire genus is apparently winter active, with a cold season reproductive peak (Kronestedt 1968; Merrett 1969; Huhta & Viramo 1979; Draney 1997b). *Centromerus sylvaticus* has a low optimal temperature for postembryonic growth, which results in slow growth during the summer months, delaying maturity until late fall or winter (Schaefer 1977). In southern England, males and females peak in December and January, and females survive until July. Our data, showing high numbers of individuals in fall and none in the spring, may indi-

cate that in harsh winter climates, reproduction occurs before winter, and adults do not generally survive to the next spring.

The four species of *Walckenaeria* in our data set all displayed a stenochronous pattern of adult activity, with short peaks occurring in late winter (Fig. 4, *W. directa*), June–July (*W. prominens*), Mid–July (*W. atrotibialis*), and early August (*W. castanea*). Examined species within the large genus *Walckenaeria* all seem to be univoltine (Tretzel 1954; Merrett 1969; Huhta & Viramo 1979; Draney 1997a); whether this trait is constant within the taxon remains to be seen.

Several authors (Schmoller 1970; Muma 1973; Doane & Dondale 1979) have suggested that the male pitfall catch peak is the best indicator of the mating period of a species, since males are trapped as a result of their mate-searching behavior. Female catch is related to either foraging behavior in order to obtain food for egg production, or behavior related to oviposition activity. In many species (such as our *P. costatus*, *L. intricatus*, and *M. viaria*, Fig. 4) the male peak occurs well before the female peak, although in other species (*A. dentisetis*, *H. insignis*, *C. sylvaticus*, *B. pallidus*, *L. zebra*, Fig. 4) the peaks are essentially simultaneous. In no species is the female peak well before the male peak; cases with earlier female peaks occur only in species with few trapped individuals, and the pattern could be a result of sampling error (e.g., *W. directa*, $n = 39$ and *D. bidentata*, $n = 38$, Table 1). Additionally, we found that more males than females were collected in our pitfall traps. This is also largely attributable to the differential locomotory activity associated with reproduction; males tend to wander extensively in search of mates. In two cases we collected more females of a species than males (Table 1). This may be due in part to oviposition behavior. For example, Toft (1978) suggested that many species, including *H. insignis*, lay their eggs in the leaf litter, even if they forage higher in the vegetation. Koponen (1987) also reported highly female-biased pitfall catches of two linyphiid species, *Hybauchenidium gibbosum* (Sørensen 1898) (95% female, $n = 127$) and *Zornella cultrigera* (L. Koch 1879) (100% female, $n = 36$).

Linyphiid spiders are important predators in northern forests, given their ubiquity, abundance, and high diversity. Phenological data can be useful to predict times during which species are likely to occur and also allow us to better predict potential biological interactions and population responses to human-caused and natural ecosystem alterations, depending on the timing of these events. Phenological data is useful but is not known with precision for most linyphiid species. Useful phenological insights can be garnered from ecological data collected for other purposes, and we hope future work will further test patterns uncovered in our study forest.

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# A REVISION OF THE SPIDER GENUS *CALILEPTONETA* PLATNICK (ARANEAE, LEPTONETIDAE), WITH NOTES ON MORPHOLOGY, NATURAL HISTORY AND BIOGEOGRAPHY

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**ABSTRACT.** The spider genus *Calileptoneta* Platnick is revised and all species are described, diagnosed and keyed. A neotype for *Calileptoneta californica* (Banks) is designated and *Calileptoneta sylva* (Chamberlin & Ivie) is removed from synonymy with *Calileptoneta californica* (Banks). The female of *Calileptoneta noyoana* Gertsch and the male of *Calileptoneta sylva* (Chamberlin & Ivie) are described for the first time. Three new species are described: *Calileptoneta briggsi*, *Calileptoneta cokendolpheri*, and *Calileptoneta ubicki*. The morphology of *Calileptoneta* is discussed, and interpretive illustrations of male and female genitalia are provided. The natural history of *Calileptoneta* is presented with an account of the mating behavior for *C. ubicki*. The distribution of *Calileptoneta* species is discussed, and areas of endemism and potentially new *Calileptoneta* species are noted.

**Keywords:** Taxonomy, new species, USA, Leptonetidae

The first North American leptonetid, *Leptoneta californica* Banks, was described in 1908 and it was not until the time of Gertsch (1974) that the first effort to comprehensively treat the fauna was performed. Although detailed studies on the European fauna (Brignoli 1972, 1974, 1975, 1976, 1977, 1979a, 1979b, 1979c; Fage 1913; Machado 1941, 1945) revealed great genitalic diversity, Gertsch relied largely on somatic characters, resulting in an inadequate description of the fauna and a series of controversial taxonomic decisions (Brignoli 1977, 1979c; Platnick 1986). Platnick (1986) reassessed the higher-level taxonomy of the North American leptonetids by using a new suite of characters involving middorsal integumentary glands and discovered support for the grouping of the North American fauna into four genera, confirming the opinions of Brignoli (1977, 1979c).

Little attention has since been paid to these spiders despite the problems found in Gertsch's (1974) monograph. Most taxa suffer from incomplete species descriptions and doubtful species limitations. Additionally, over 50% of the specimens studied by Gertsch (1974) are juveniles that cannot be diagnosed. This situation is especially troubling in western North America, where the bulk of leptonetid diversity is found in environmentally sensitive areas, and where a complete knowledge of these taxa may contribute to conservation efforts.

The major systematic problem of the North American leptonetids is an incomplete understanding of their genitalic morphology. A survey of the European literature reveals a variety of genitalic characters, especially on the male palpal bulb. None of the literature treating the North American fauna sufficiently illustrates the complexity of the male genitalia, and the females are ignored almost entirely. Not only does this lack of information miss a suite of informative characters, it may also underestimate the true diversity of the fauna.

This study reexamines the genus *Calileptoneta* Platnick 1986 and builds on the findings of Gertsch (1974) by using detailed genitalic examinations, natural history observations and additional specimens collected since his monograph. Three new species are described, including the first troglobitic *Calileptoneta*. Natural history observations are included, with the first account of the mating behavior of leptonetids and a description of their web architecture. The biogeography of *Calileptoneta* is also discussed, noting areas of endemism and localities that may yield additional species. It is

Table 1.—List of anatomical abbreviations used in the text and figures.

| | |
|---|---|
| AC | apical constriction |
| AEG | anterior eye group |
| AER | anterior eye row |
| ALE | anterior lateral eyes |
| ALS | anterior lateral spinnerets |
| AME | anterior median eyes |
| AH | apical hook |
| AL | accessory lobe |
| E | embolus |
| OA | ocular area |
| OAL | ocular area length |
| OAW | ocular area width |
| PBP | proximal bulb process |
| PEG | posterior eye group |
| PF | proapical flange |
| PL | prolateral lobe |
| PLE | posterior lateral eyes |
| PLS | posterior lateral spinnerets |
| PMS | posterior median spinnerets |
| PS | paraembolar setae |
| RS | retroapical seta |
| S | spermathecae |

the aim of this study to provide a guideline for the revision of the other North American leptonetids, and contribute to an eventual understanding of their phylogenetic history.

## METHODS

Each species is thoroughly described, diagnosed, and keyed. Species descriptions refer to a single adult individual for each sex, which is identified as a type or by the locality at which it was collected. Descriptions of females and all previously unknown sexes were written using specimens collected in association with diagnosable individuals at or near the type locality. In cases of sympatry [*C. californica* (Gertsch 1974) and *C. helferi* Gertsch 1974)], descriptions were based upon associated individuals collected as close to the type locality as possible. Anatomical abbreviations used in the text are listed in Table 1. All measurements are in mm and quantify the size of a structure at its widest or longest point. A section reporting the variation in the most conspicuous and variable features follows each description and represents two to nine individuals (*n*), encompassing the full range in overall size. All illustrations are by Virginia Kirsch (VK) or myself (JL) and are attributed in the figure captions.

Prior to examination with a Hitachi S-520 or Leo 1450VP Scanning Electron Microscope, all structures were briefly cleaned in an ultrasonicator and critical point dried. Spinneret preparations followed the methods of Coddington (1989), consisting of a brief cleaning in an ultrasonicator and a gentle squeeze of the abdomen using forceps in order to extend and separate the spinnerets. Large structures were examined using Olympus SZH10 and Leica SMZ10 microscopes.

Vulvae were carefully excised and placed in a trypsin solution for 2–8 hours under a heat lamp to digest extraneous tissue. If characters remained unclear, the vulva was stained with Chlorazol Black and reexamined. Photographs were taken using an Olympus PM-10AK and a Nikon Coolpix 990 digital camera attached to a Nikon SL3D® microscope. All genitalia and small structures were placed in Hoyer's solution or glycerin and examined in temporary mounts following the procedure described by Coddington (1983), under a Nikon SL3D® microscope.

Palpal structures are provided names based on the nomenclature used by Gertsch (1974) and Platnick (1986), when the structure referred to was unambiguously identified. Structures not previously discussed in the literature treating the North American fauna were given names based on their relative location on the palpal bulb. I did not use names provided in literature treating the European or Asian faunas. Such a system would imply homology of structures where none is intended. It is not the aim of this study to establish a precedent for the nomenclature of leptonetid genitalia, except in that structures should be clearly labeled and illustrated.

The specimens on which this study was based were kindly provided by Norman Platnick, American Museum of Natural History (AMNH), Laura Leipensburger, Museum of Comparative Zoology (MCZ), Fred Coyle, Western Carolina University (WCU), James Cokendolpher, personal collection (JC), and Darrell Ubick, personal collection (DU). Additional material is from the collection of the California Academy of Sciences (CASC).

## SOMATIC MORPHOLOGY

**Cephalothorax.**—The carapace (Figs. 8, 10) is domed and gently sloping posteriorly in lateral profile. The color is pale yellow with

Figure 1.—Web of ***Calileptoneta ubicki*** new species from Arroyo Seco Canyon. Scale bar = 2.0 mm.

purple-brown dusky markings surrounding the eyes and carapace margins. The fovea is a longitudinal purple-brown dusky band (Figs. 2, 4, 6). The eyes are relatively large (except in *C. briggsi* new species), and raised above the carapace in lateral profile (Figs. 8, 10). Setation is minimal, although a series of thin, elongate setae occur posteriad of the PME, and a distinct pair of crossing setae are at the apex of the clypeus (Figs. 2, 4, 6). The sternum (Fig. 9) is slightly domed in lateral profile (Fig. 10) and the palpal coxae bear a serrula extending the length of the anterior edge (Fig. 11). The chelicerae (Figs. 15–23) have a promargin with a single row of large teeth on a fine ridge, and a retromargin with 1–7 denticles. As with other leptonetids, the promargin bears a relatively large proximal tooth, although *C. noyoana* (Gertsch 1974) and *C. wapiti* (Gertsch 1974) males have a diagnostic enlarged tooth distally (Figs. 18, 19).

**Legs.**—The legs are long and thin with a regular series of slender spines on the tibiae and metatarsi and a single apical spine on the patellae (Figs. 3, 5, 7). Sexual dimorphism of the legs is minimal, with the leg length of males only slightly longer than that in females. A point of weakness occurs at the patella-tibia joint, resembling linyphiid, hersiliid and filistatid spiders, and the legs are readily dropped distad of this joint by living specimens (pers. obs.). A small preening comb consisting of 6 paired setae occurs ventroapically on the metatarsus (Figs. 12, 13). The comb is often tucked into the tibia-metatarsus joint and may require the removal of one of the segments to be clearly viewed. Similar combs have also been recorded in *Appaleptoneta* and *Neoleptoneta* (Cokendolpher pers. comm.) and may be a synapomorphy uniting leptonetids as a whole. The integumentary glands discussed by Platnick (1986), occur middorsally on the femora, patellae and tibiae of all legs, including the palpi. The sinuous patellar gland plates with large pores (Fig. 14) (Platnick, 1986 figs. 55–60) may indeed serve to unite *Calileptoneta*, although several other gland types were found on *Calileptoneta* species. No less than four different types of glands were found on the legs of *Calileptoneta sylva* (Chamberlin & Ivie 1942), including gland types suggested as synapomorphies for other taxa by Platnick (1986)

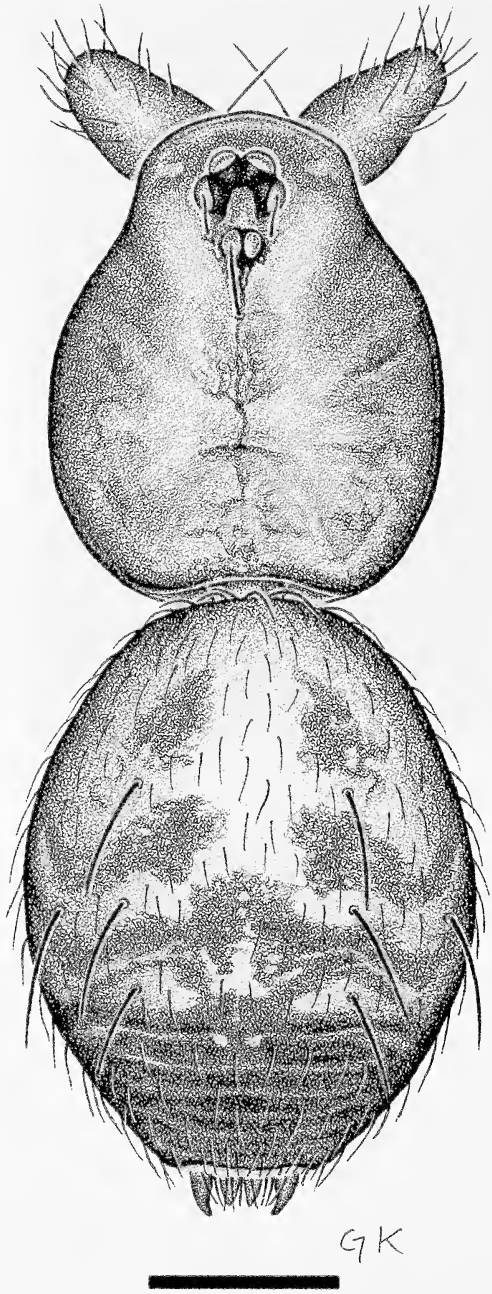



Figure 2.—***Calileptoneta ubicki*** new species, male, dorsal from Arroyo Seco Canyon. Scale bar = 0.5 mm. Illustration by VK.

(Ledford & Ubick, pers. obs.). The tarsal claws are simple, with few teeth.

**Abdomen.**—The abdomen (Figs. 2–7) is oval in shape, with several long, slender setae dorsally. The color is pale with a series of dusky chevron markings. These markings were used by Gertsch (1974) to diagnose species (especially juveniles) but I found them highly variable within species.

**Spinning organs.**—The spinnerets (Figs. 24–31) of *Calileptoneta* are typical of other leptonetids and do not substantially differ from the findings of Platnick et. al. (1991). The ALS (Figs. 25, 30) are circular in apex outline, with 6–10 pustulose tartipores. The posterior spinnerets (Figs. 26, 27, 31) are highly modified, forming elongate, narrow tetrahedrons bearing 1–2 rows of spigots with short, circular bases and narrow shafts. The PLS of females bear 1–2 elongate spigots with thick shafts (Fig. 31) that presumably serve the cylindrical glands (Platnick et. al. 1991). No such spigots were found in males, nor were any nubbins. A series of four epiandrous spigots (Fig. 28) occur at the apical edge of the epigastric furrow in males.

## GENITALIA

**Male.**—The male genitalia (Figs. 32–94) of *Calileptoneta* are intricate structures that require careful observation under compound microscopy in order to be viewed properly. The palpal segments vary greatly in length, with some species (*C. helferi*, *C. noyoana*) having elongate femora and patellae (Figs. 5, 7) several times the carapace width. The palpal tarsus bears an apical constriction (AC, Figs. 32, 35, 38) with a single seta retroapically (retroapical seta, RS, Figs. 33, 37, 39). Small groups of modified setae occur on the retrolateral surfaces of the tibiae and tarsi (Figs. 37, 40, 68, 71, 86, 92). Spination is variable with *C. briggsi*, *C. californica*, *C. helferi* and *C. sylva* bearing numerous spines on the pro-and retrolateral surfaces of the palpal femora (Fig. 7), and *C. cokendolpheri* new species, *C. noyoana*, *C. oasa* (Gertsch 1974), and *C. ubicki* new species, lacking palpal spines entirely (Figs. 3, 5). The bulb is suboval in shape and lightly sclerotized. As reported by Brignoli (1979c), the bulb is expandable, and may rotate up to 90° during mating. An unusual prolongation of the palpal bulb (proximal bulb process, PBP, Figs. 38–40, 41–43, 47–49, 59–61, 77–79) extends proximally on *C. briggsi*, *C. californica* (Gertsch, 1974), *C. helferi* and *C. sylva*, and may function as an anchoring point during mating. The prolateral lobe (PL, Figs. 32, 35, 38), first proposed as a synapomorphy for *Calileptoneta* by Platnick (1986), is a dorsal ex-

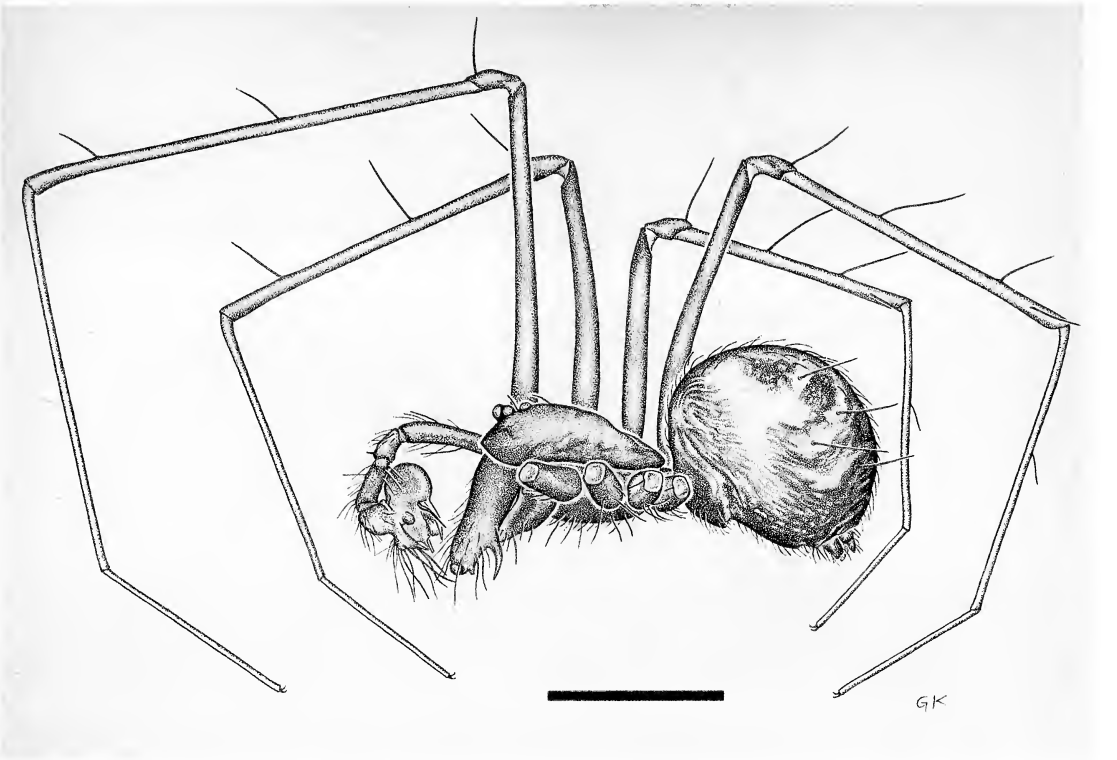



Figure 3.—***Calileptoneta ubicki*** new species, male, lateral from Arroyo Seco Canyon. Scale bar = 1.0 mm. Illustration by VK.

tension of the bulb (not the tarsus) that may serve as a point of rotation during bulb expansion. An accessory lobe (AL, Figs. 46, 82) occurs distad of the PL, and gradually tapers into a small hook at its apex (apical hook, AH, Figs. 35, 38, 46, 52, 56, 82, 87, 94). The ventroapical surface of the bulb is divided by a narrow ridge (Fig. 45) that is produced into a translucent, spoon-shaped, proapical flange with serrate edges (proapical flange, PF, Figs. 33, 36, 39). The prolateral surface of the ridge is deeply striate (Figs. 45, 46, 51, 52, 63, 64, 76, 82), composed of numerous laterally fused setae. The embolus (E, Figs. 33, 36, 39) is situated ventroapically and tapers into a point (Figs. 75, 76) or a broad fork (Fig. 46). An adjacent group of twisted circular or fan-like setae (paraembolar setae, PS, Figs. 32, 34, 35, 38, 39) occur prolaterad of the embolus and may be the remnants of the laterally fused setae on the prolateral surface of the bulb. The tarsal organs (Figs. 95–97) of *Calileptoneta* are cylindrical structures situated at the apex of the palpal tarsus, and vary in the degree by which they extend from the tarsus.

**Female.**—The female genitalia (Figs. 98–118) of *Calileptoneta* are relatively uniform, and of little diagnostic value. Although many diagnostic characters were discussed by Gertsch (1974), most of his illustrations were drawn incorrectly and are misleading. The lack of diagnostic information in females was especially problematic during the course of this study, and all species except for *C. cokendolpheri*, *C. oasa* and *C. ubicki* remain undiagnosable in the absence of associated males. The atrium is triangular or trapezoidal with a dense network of striae (Figs. 102, 104, 106, 109–118) ventrally and a lateral pair of tightly twisted spermathecae (S, Figs. 98, 101) that connect dorsally via a sharp bend (Figs. 101, 107, 108). This bend is often difficult to observe and requires careful preparation to be viewed clearly (see Methods section for a discussion of techniques that aid in the examination of leptonetid genitalia). Two species, *C. oasa* and *C. ubicki*, have an atrium with a distinctive apical bifurcation (AB, Figs. 98, 102, 104) although this is less pronounced in *C. oasa*.

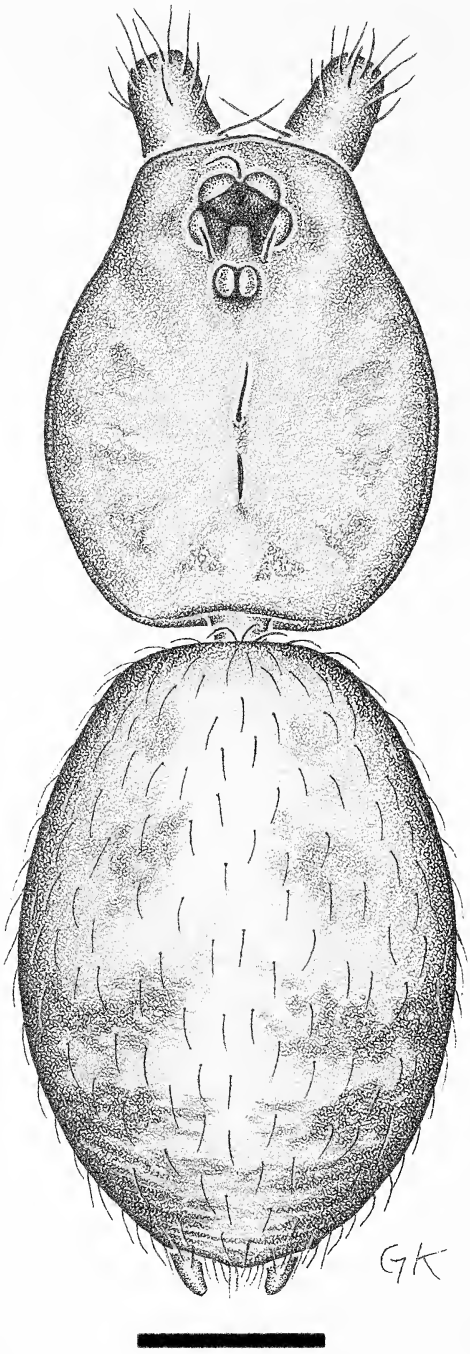



Figure 4.—*Calileptoneta noyoana* (Gertsch), male, dorsal from Fort Bragg. Scale bar = 0.5 mm. Illustration by VK.

## NATURAL HISTORY

**General behavior and web architecture.**—*Calileptoneta* are small spiders, generally restricted to cool, moist microenvironments such as caves, leaf-litter and deeply imbedded rock outcrops. They are rarely collected due to their cryptic nature and temporal occurrence, especially in areas that are seasonally arid. Individuals appear to congregate in ideal habitats and, at the correct time of year, may be collected in large series. The web (Fig. 1) of *Calileptoneta* is a rectangular, finely woven sheet 3–4cm in diameter, presumably constructed with the highly modified PLS. Individuals hang beneath the sheet and readily drop from the web into a defensive posture whereby the legs are drawn close to the body when disturbed (pers. obs.).

**Mating behavior.**—A captive group of *C. ubicki* were kept in a small plastic container containing sphagnum moss and fed a diet of freshly killed *Drosophila* for several months. Up to 7 individuals occupied the same container and overlapping sheet webs were constructed with individuals often resting in close proximity. An adult pair of *C. ubicki* was removed from the group and several instances of mating were recorded. Courtship displays consisted of a slight plucking of the female's web by the male using his palpi. Both individuals remained inverted beneath the sheet as the male slowly approached. Upon contact, a single palpal bulb rotated 90° before being inserted into the atrium and then exchanged for the other bulb. Alternate bulb insertion lasted approximately 5–10 seconds and mating was completed after 30 minutes. The male situated himself in the female's web for several hours following mating. No sperm web was recorded for the male and the female did not construct any eggsacs.

## BIOGEOGRAPHY

The distribution of *Calileptoneta* (Figs. 119–122) is largely vicariant with most species restricted to a particular locality or habitat type. This is not surprising given their general biology and the similar patterns of endemicity exhibited by other leptonetid taxa (Brignoli 1974, 1977; Gertsch 1971). Sympatric populations are known, however, and a strict hypothesis of vicariance may be premature given the poor sampling in central Oregon, eastern California and southern California (Fig. 122).

The restriction of *Calileptoneta* species to specific habitat types is of special interest as environmental concerns are paramount in California and Oregon. Of particular importance

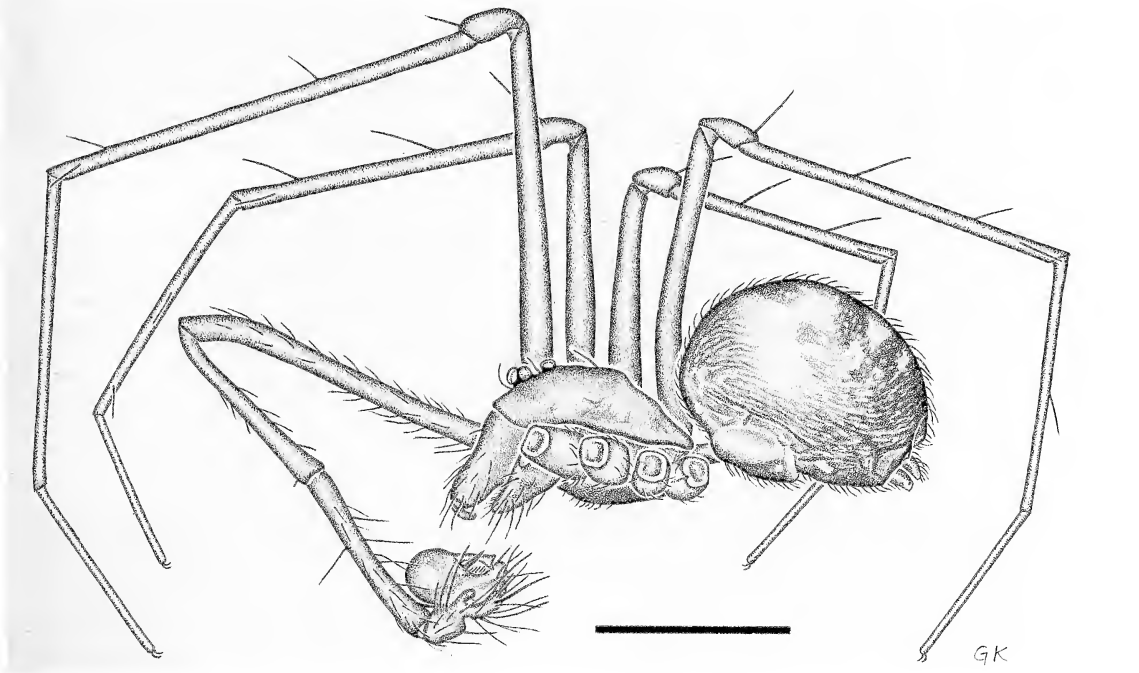



Figure 5.—*Calileptoneta noyoana* (Gertsch), male, lateral from Fort Bragg. Scale bar = 1.0 mm. Illustration by VK.

are the distributions of *C. noyoana* and *C. cokendolpheri*, which are endemics of economically important forest types-redwood forest and Douglas Fir forest, respectively. Although not particularly charismatic, nor common enough for use as indicators, these species contribute to the knowledge of biodiversity in these forests and may assist conservation efforts.

Troglobitic species regularly receive special conservation status due to their extremely limited distributions and sensitivity to disturbance. It is surprising that only a single troglobitic *Calileptoneta* is known, despite California's rich cave fauna and in contrast to the other major karst regions in the Nearctic, Texas and Appalachia, which have numerous cavernicolus leptonetids. In California, this niche appears to be occupied by the many cavernicolus telemids, which do not occur in the eastern United States (D. Ubick pers. comm.). *Calileptoneta briggsi* is restricted to a poorly known cave system that receives little attention from cavers and is probably not at risk. Additional troglobitic *Calileptoneta* almost certainly occur, and indeed two female specimens have been collected in caves from Caleveras and Tulare counties in eastern California (Fig. 122). Given the large disjunction between these specimens and other known populations of *Calileptoneta*, they almost certainly represent new species.

Undiagnosable females and juveniles (Fig. 122) provide additional interesting distributional data for *Calileptoneta*. Not only do these specimens contribute to a broader understanding of the distribution of *Calileptoneta*, they reveal distributional gaps that may yet yield additional species. The gap in southern California is the most striking, with only two species, *C. ubicki* and *C. oasa*, known from the entire southern half of the state. The seasonally arid climates of these areas makes the collection of specimens unpredictable, but given the habitat diversity and faunistic richness of these areas, the possibility of this being a natural distributional gap is unlikely. The large gap in Oregon from Josephine County to Lane County is also probably artificial considering the rich oak woodland and riparian areas that occur between these two counties.

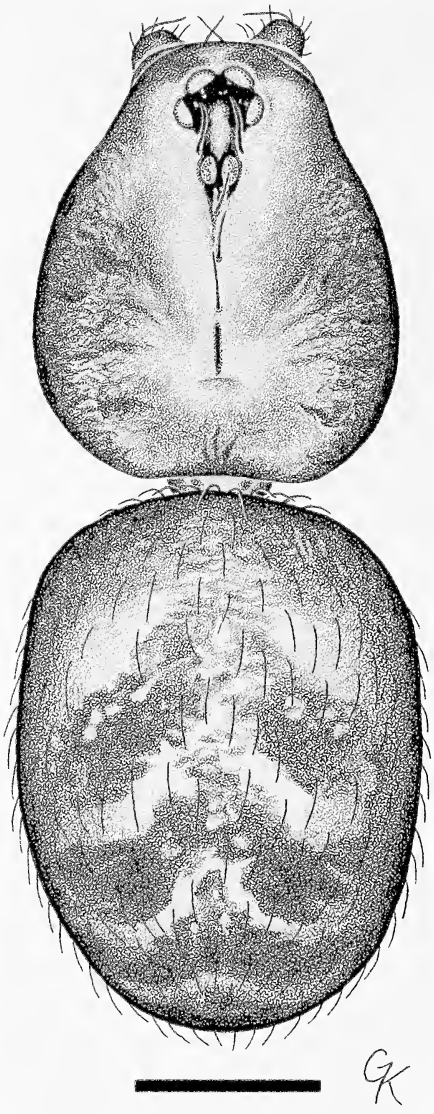


Figure 6.—*Calileptoneta helferi* (Gertsch), male, dorsal from Mt. Diablo. Scale bar = 0.5 mm. Illustration by VK.

## DISCUSSION

Perhaps the largest remaining gap in the knowledge of the North American leptonetids is an understanding of their phylogentic affinities. Not only would a phylogeny for these spiders reveal interesting evolutionary patterns within North America, it would also contribute to an understanding of leptonetid relationships as a whole. Such a study would require a comprehensive review of all North American leptonetid genera, and inclusion of potential European and Asian outgroup taxa, which is beyond the scope of this study. The relationships within *Calileptoneta* also need further investigation and future work will be directed at this goal. Additional fieldwork is prerequisite to this understanding, especially in the distributional gaps of central Oregon, southern California and eastern California. Additional specimens will also facilitate the diagnosis of females, particularly between *C. briggsi*, *C. californica*, *C. helferi* and *C. noyoana*. The recollection of *C. wapiti* also must take priority, as will the discovery of males at cave sites in Calaveras and Tulare counties.

## TAXONOMY

### FAMILY LEPTONETIDAE

### Genus *Calileptoneta* Platnick 1986

*Leptoneta* (in part): Banks 1910: 6; Brignoli 1977: 215–217; Comstock 1913: 307; Fage 1913: 566; Moles 1921: 40; Gertsch 1974: 191–192.
*Calileptoneta* Platnick 1986: 15; Platnick 2002.

**Type species.**—*Leptoneta californica* Banks 1904: 333, by original designation.

**Diagnosis.**—Distinguished from other North American leptonetid genera (*Archoleptoneta* Gertsch 1974, *Neoleptoneta* Brignoli 1972, *Appaleptoneta* Platnick 1986) by having a prolateral lobe on the male palpal tarsus (Figs. 32, 35, 38) and by the sinuous patellar gland plates bearing large pores (Fig. 14, Platnick 1986, figs. 55–60).

**Description.**—Total length 1.20–3.04. Carapace oval in dorsal view (Fig. 8), length 1.20–1.32 × width, height 0.26–0.54 × width; smooth; thoracic fovea a thin dusky band (Figs. 2, 4, 6); carapace posterior margin straight to sinuous (Figs. 2, 4, 6, 8); carapace with 2 setae posteriad of AER, 3 setae posteriad of PME, extending linearly to fovea; clypeus with 2 setae crossing distally (Figs. 2, 4, 6); six eyes, PME absent; AEG with dark markings surrounding eyes, u-shaped at posterior margin (Figs. 2, 4, 6, 8); PEG with dark circular markings surrounding eyes (Figs. 2, 4, 6); OA longer than wide, OAL 0.60–1.40 × OAW, PME 0.40–0.70 × PLE interdistances; clypeal height 0.70–1.02 × PME diameter, chelicerae unmodified, fang furrow a narrow ridge with 3–9 large teeth, retromargin with 1–5 denticles (Figs. 15–23). Sternum smooth, oval, broadly rounded posteriorly, margin entire, length 1.0–1.2 × width. Abdomen (Figs. 2, 4, 6) oval, pale, with dusky

chevron markings, and covered with fine, elongate setae. Spinning organs (Figs. 24–31) with the ALS not modified and bearing several pustulose tartipores; PMS and PLS highly modified, tetrahedral, forming a narrow ridge on surface; PMS with 2 longitudinal rows, and PLS with a single longitudinal row of spigots on short, circular bases; prolateral edge of PLS in females with 2 isolated spigots on elongate, thick bases (Fig. 31); males with 4 epiandrous spigots (Fig. 28) at the apex of the epigastric furrow. Leg formula I, IV, III, II; elongate and thin; femur I of males 2.09–3.4 × carapace width, females 1.32–2.71 × carapace width; middorsal integumentary glands sinuous, with large pores (Fig. 14); preening comb consisting of 6 paired setae at the apices of the metatarsi on legs I–IV (Figs. 12, 13); autospasy occurs at patella-tibia joint. Leg spination I–IV: patella d1, tibia d1–1, p1, r1. Male palpal femur length 0.67–2.78 × carapace width; palpal tarsus with a retroapical seta (Figs. 33, 37, 39). Bulb expandable, lightly sclerotized, suboval, longer than wide, length 0.40–2.20 × tibia length; with a fine ridge ventroapically, and a transparent proapical flange with serrate edges (Figs. 33, 36, 39); prolateral surface bearing a large lobe (Figs. 32, 35, 38), with a small lobe apicad (Figs. 46, 82) that is produced distally into a hook (Figs. 35, 38, 46, 52, 56, 64, 82, 87, 94); embolus ventrally situated (Figs. 33, 36, 39), with a prolateral group of twisted circular or fan-like paraembolar setae (Figs. 32, 34, 35, 38, 39); tarsal organ (Figs. 95–97) cylindrical. Female genitalia (Figs. 98–118) with a triangular or trapezoidal atrium, length 0.72–1.12 × width, densely striate on ventral surface; spermathecae situated laterally, elongate, twisted, attaching to atrium dorsally by a sharp lateral bend (Figs. 101, 107, 108).

**Distribution.**—Southern California (Riverside County) to Central Oregon (Lane County) (Figs. 119–122).

## KEY TO SPECIES OF THE GENUS *CALILEPTONETA*

The key has been written to maximize accuracy and efficiency. Multiple features are presented in each couplet in order to assist the identification of variable and poorly preserved specimens. Most taxa require high magnification under compound microscopy to insure positive identification.

### Males

1. Proximal bulb process present (Figs. 38–40), retroapical seta straight (Figs. 33, 39), pro- and retrolateral surfaces of palpal femur heavily spined (Fig. 7) ..... 2
   Proximal bulb process absent (Figs. 32–37), retroapical seta straight to curved (Fig. 37), palpal femur weakly spined or lacking spines entirely (Figs. 3, 5) ..... 5
2. Proximal bulb process elongate, length 1.0–2.04 × bulb width (Figs. 47–49, 59, 61), accessory lobe reduced (Figs. 52, 64) ..... 3
   Proximal bulb process shorter, length 0.55–1.0 × bulb width (Figs. 41–43, 77–79), accessory lobe normal (Figs. 46, 82) ..... 4
3. Palpal tibia elongate, length 1.02–1.19 × carapace width, proximal bulb process extending ½–¾ length of tibia, bulb length 0.81–1.04 × tibia length (Figs. 6–7, 59–64), body darkly pigmented ..... *C. helferi* (Gertsch)
   Palpal tibia shorter, length 0.76–0.90 × carapace width, proximal bulb process extending entire length of tibia, bulb length 1.09–1.40 × tibia length (Figs. 47–52), body lightly pigmented ..... *C. californica* (Banks)
4. Body pigmentation entirely lacking, eyes reduced and flattened, femur I elongate, length 2.88–3.40 × carapace width; proximal bulb process longer, length 0.85–1.0 × bulb width (Figs. 41–43), embolus apically forked (Fig. 46) ..... ***C. briggsi*** new species
   Body darkly pigmented, eyes normal, diameter PME 0.50–0.64 × PLE interdistances; proximal bulb process shorter, with slight retrolateral bend (Fig. 78), length 0.55–0.86 × bulb width (Fig. 79) ..... *C. sylva* (Chamberlin & Ivie)
5. Palpal tarsus with a retrolateral pair of twisted setae (Figs. 37, 65–70, 92), chelicerae with an enlarged distal tooth (Figs. 18, 19), retrodistal cheliceral process absent ..... 6

Palpal tarsus lacking twisted setae, chelicerae without an enlarged distal cheliceral tooth (Figs. 15–17, 20–23), retrodistal cheliceral process present (Fig. 16) or absent ..... 7

6. Palpal segments elongate, femur length 2.24–2.78 × carapace width (Figs. 5, 65–70) .... ..... *C. noyoana* (Gertsch)
Palpal segments normal, femur length 0.63–1.0 × carapace width (Fig. 89–94) ..... ..... *C. wapiti* (Gertsch)

7. Bulb bearing two proapical flanges; proximal flange setose, distal flange tightly curled (Fig. 54); embolus hook-shaped (Fig. 56) ..... ***C. cokendolpheri*** new species
Bulb with single proapical flange, lacking setae, apex loosely to tightly curled (Figs. 75, 76, 88), embolus tapering to fine point (Figs. 75, 76) ..... 8

8. Retrodistal cheliceral apophysis present (Fig. 16), with a whip-shaped seta retroapically on the palpal tibia (Fig. 86), proapical flange sinuate (Fig. 88) ..... ***C. ubicki*** new species
Retrodistal cheliceral apophysis absent (Fig. 15), with a hook-shaped seta retroapically on the palpal tibia (Fig. 71), proapical flange straight (Fig. 75) ..... *C. oasa* (Gertsch)

Females

1. Atrium with an apical bifurcation (Figs. 98, 102, 104) ..... ..... *C. oasa* (Gertsch), ***C. ubicki*** new species
Atrium entire (Figs. 99, 100, 106, 109–118) ..... 2

2. Atrium (Figs. 99, 100, 106, 109–116) distinctly triangular, tapering to a point apically, with normal base ..... ... ***C. briggsi*** new species, *C. californica* (Banks), *C. helferi* (Gertsch), *C. noyoana* (Gertsch), *C. wapiti* (Gertsch)
Atrium (Fig. 117–118) trapezoidal, apically subquadrate, with broad base, atrium length 0.72–0.81 × width ..... ***C. cokendolpheri*** new species

### *Calileptoneta briggsi* new species
Figs. 22, 41–46, 111, 112, 121

**Type material.**—Male holotype from Indian Valley Creek Cave, Trinity County, California, USA, 40°37′N, 123°27′W, 27 October 1990, D. Ubick, W. Rauscher (CASC). Paratypes: USA: *California*: 2♂, 5 ♀, same data as holotype (CASC; 1 ♂, 1 ♀, DU).

**Other material examined.**—USA: *California*: Trinity County: Indian Valley Creek Caves, 4 air miles SSE. Hyampom, 40°37′N, 123°27′W, ~1800 ft. elevation, 5 July 1980, T. Briggs, W. Ma, W. Rauscher (2 ♀, 1 juvenile, AMNH), 27 October 1990, D. Ubick, W. Rauscher (4 juveniles, CASC), 31 August 1996, D. Ubick (2 juveniles, DU); Lower Butter Creek Cave, 40°37′N, 123°27′W, 5 July 1980, T. Briggs, W. Ma, W. Rauscher (2 ♀, 4 juveniles, AMNH).

**Etymology.**—This species is named in honor of Dr. Tom Briggs, discoverer of this and many other troglobitic arachnids throughout California.

**Diagnosis.**—Distinguished from all other *Calileptoneta* by lacking pigmentation and having the eyes greatly reduced and flattened. *Calileptoneta briggsi* may be further separated from other *Calileptoneta* males, except *C. californica*, *C. helferi* and *C. sylva*, by having a proximal bulb process (Figs. 38–43), and a straight retroapical seta (Figs. 39, 48); from *C. californica* and *C. helferi* by having the proximal bulb process (Figs. 77–79) short, process length 0.85–1.08 × bulb width, and having the prolateral apical lobe large (Figs. 46, 82); from *C. sylva* by having an elongate femur I, length 2.88–3.40 × carapace width, and an apically forked embolus (Fig. 46).

**Male (holotype).**—Total length 2.64. Specimen pale, entirely lacking pigmentation. Carapace 1.19 long, 0.93 wide, height at fovea 0.33 × carapace width; clypeus 0.17 high, chelicerae 0.66 long, fang furrow with 9 teeth on a narrow ridge and 5 denticles on retromargin (Fig. 22). Ocular area 0.23 long, 0.17 wide; diameter PME 0.50 × PLE interdistances. Sternum 0.65 long, 0.17 wide; labium 0.08 long, 0.16 wide; palpal coxae 0.54 long, 0.20 wide.

Spination: palpus: femur p1-1-2-1-2-2-2-2-3-4-1, r3-2-1-1-2-3-2; patella d1; tibia r3; tarsus r1 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [To-

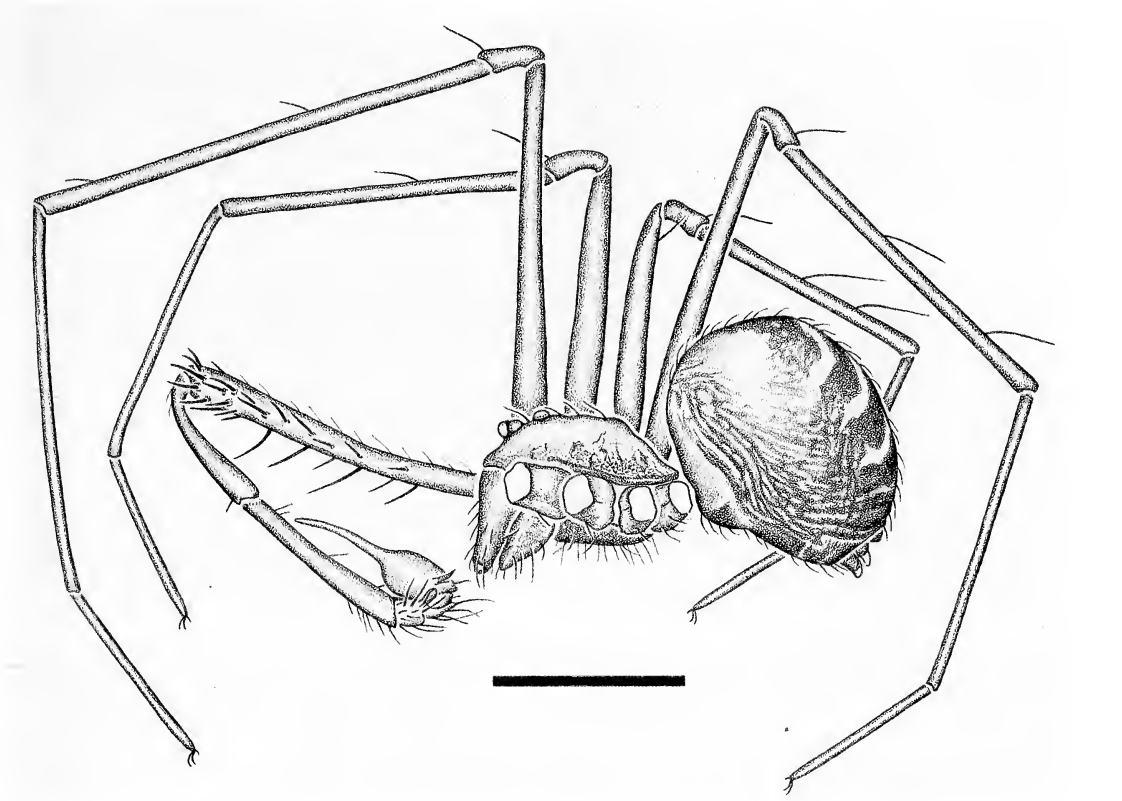


Figure 7.—*Calileptoneta helferi* (Gertsch), male, lateral from Mt. Diablo. Scale bar = 1.0 mm. Illustration by VK.

tal]): I: 3.17 + 0.39 + 2.80 + 2.24 + 1.34 = [9.95]; II: 1.90 + 0.34 + 2.04 + 1.73 + 1.10 = [7.12]; III: 1.70 + 0.27 + 1.59 + 1.46 + 0.90 = [5.90]; IV: 2.10 + 0.32 + 2.15 + 1.93 + 1.15 = [7.65]; pedipalpus: 1.08 + 0.44 + 0.66 + 0.41 = [2.60]. Femur I 3.40 × carapace width, palpal femur 1.16 × carapace width.

Palpal bulb (Figs. 41–46) 0.79 long, 0.27 wide; palpal tibia with a retroapical group of stiff setae; proximal bulb process (Figs. 41–43) short, reaching to base of tibia, bulb length 0.98 × length tibia; embolus broadly forked at apex (Fig. 46); paraembolar setae circular, distally broad, reaching slightly beyond base of fork on embolus (Fig. 46); accessory lobe large (Fig. 46).

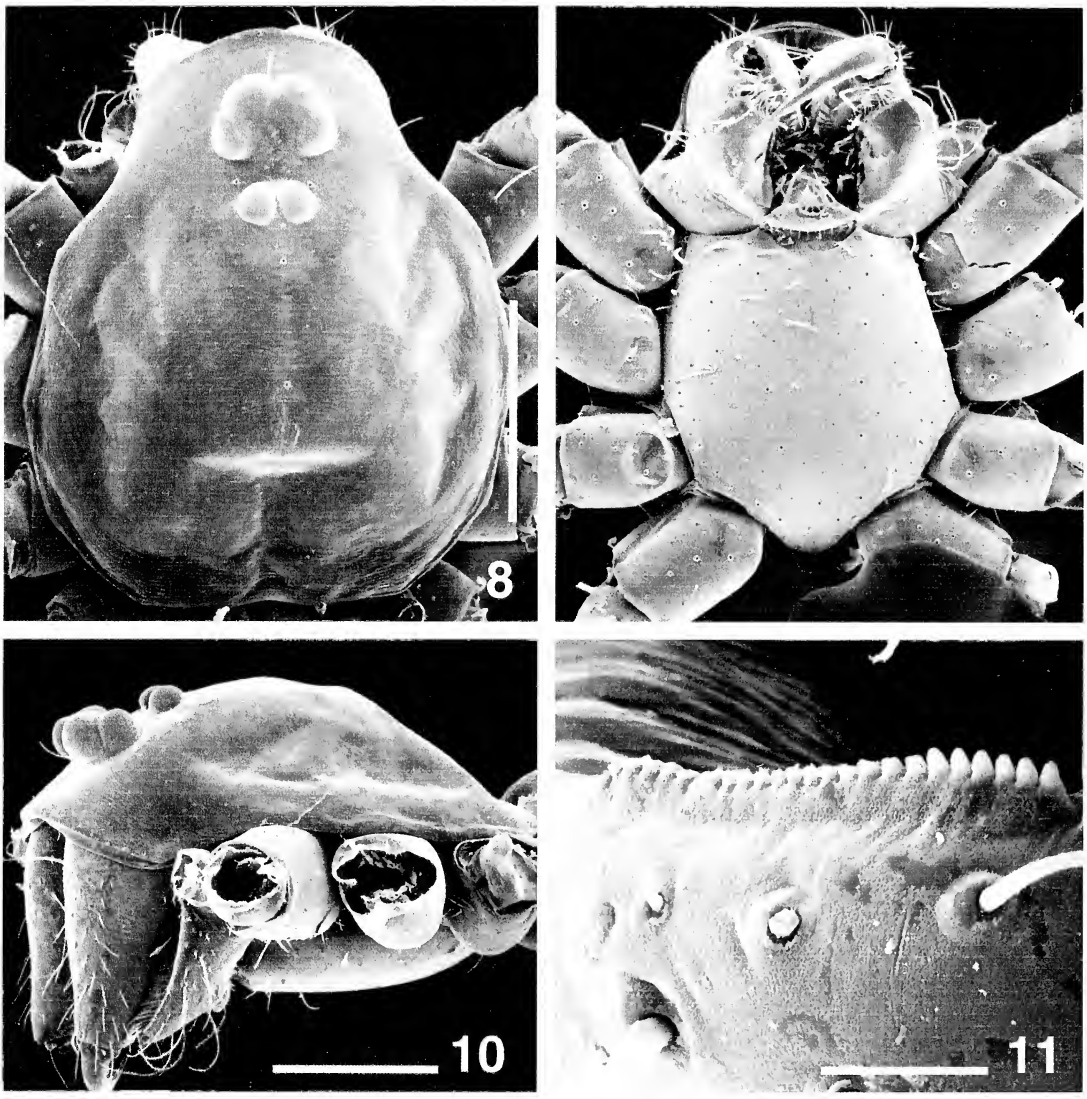
Abdomen pale, without pattern, 1.45 long, 1.22 wide.

**Variation (*n* = 2).**—Total length 2.05–2.64; carapace length 1.24–1.31 × carapace width; OAL 1.35–1.77 × OAW, diameter PME 0.40–0.53 × PLE interdistances; length femur I 2.10–3.40 × carapace width, palpal femur 0.91–1.20 × carapace width; palpal bulb length 1.15–1.36 × palpal tibia length; proximal bulb process length 0.85–1.08 × bulb width.

**Female (paratype).**—Total length 2.90. Coloration and markings same as male.

Carapace 1.2 long, 0.93 wide, height at fovea 0.34 × carapace width; clypeus 0.17 high, chelicerae 0.65 long, fang furrow with 8 teeth on a narrow ridge and 4 denticles on retromargin (Fig. 22). Ocular area 0.11 long, 0.18 wide; diameter PME 0.50 × PLE interdistances. Sternum 0.77 long, 0.70 wide; labium 0.14 long, 0.20 wide; palpal coxae 0.49 long, 0.23 wide.

Spination: palpus: patella d1 (apical), tarsus p3-1-1, r1-4, v1. Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 2.32 + 0.34 + 2.93 + 1.98 + 1.27 = [8.84]; II: 1.93 + 0.34 + 1.98 + 1.63 + 1.02 = [6.9]; III: 1.63 + 0.29 + 1.49 + 1.46 + 0.90 = [5.77]; IV: 2.15 + 0.29 + 2.10 + 1.88




Figures 8–11.—*Calileptoneta* sp., female from Mt. Diablo. 8. Carapace, dorsal. 9. Cephalothorax, ventral. 10. Cephalothorax, lateral. 11. Right palpal coxa showing serrula. Scale bars: A–C = 270 μm, D = 20 μm.

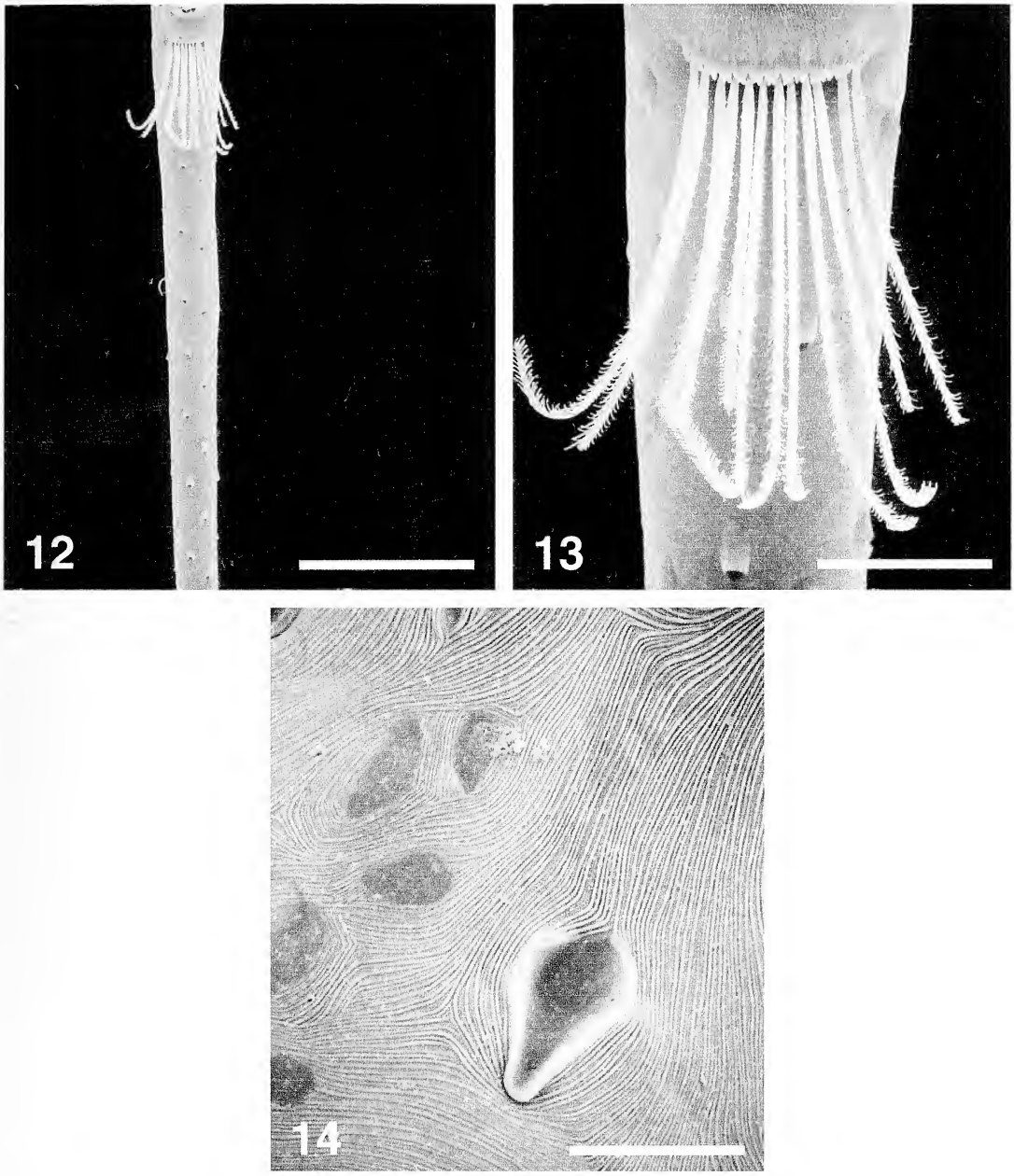
+ 1.12 = [7.54]; pedipalpus: 0.80 + 0.23 + 0.61 + 0.70 = [2.34]. Femur I 2.50 × carapace width, palpal femur 0.86 × carapace width.

Abdomen pale, without pattern, 1.7 long, 1.35 wide. Atrium 0.18 long, 0.23 wide, spermathecae 0.18 long (Figs. 111–112).

**Variation ($n$ = 3).**—Total length 2.63–3.04; carapace length 1.26–1.32 × carapace width; OAL 0.60–1.45 × OAW, diameter PME 0.40–0.50 × PLE interdistances; length femur I 2.5–2.71 × carapace width, palpal femur 0.82–0.89 × carapace width; atrium length 0.78–0.91 × width, spermathecae 0.78–0.80 × atrium width.

**Natural history.**—These spiders were collected hanging from sheet webs among a root mass in the cave's dark zone. Given the lack of pigmentation, reduced eyes, and elongate legs of this species, it is considered a troglobite.

**Distribution.**—Known only from Indian Valley Creek Caves which include Indian Valley Creek Cave and the adjacent Lower Butter Creek Cave in Trinity County (Fig. 121). These caves occur along a continuous band of




Figures 12–14.—*Calileptoneta* sp., female from Mt. Diablo. 12–13. Left metatarsus III, showing preening comb. 14. Middorsal integumentary gland, left leg III. Scale bars: A = 150 μm, B = 38 μm, C = 7.5 μm.

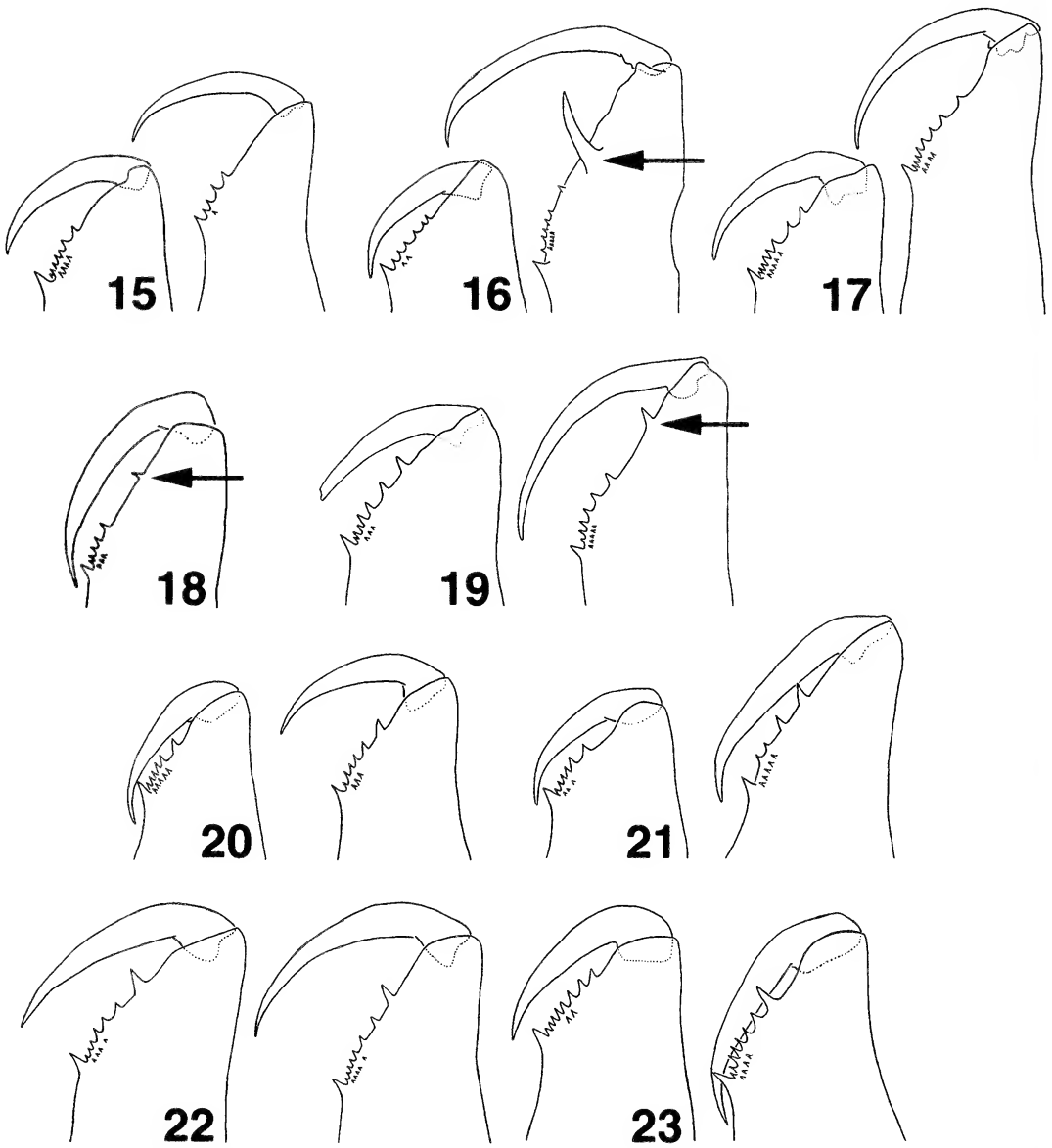
limestone and were presumably once connected (T. Briggs, D. Ubick pers. comm.).

*Calileptoneta californica* (Banks 1904)
Figs. 20, 38–40, 47–52, 115, 116

*Leptoneta californica* Banks 1904: 333; Banks 1910: 6; Brignoli 1977: 217; Comstock 1914: 307; Fage 1913: 566; Moles 1921: 40; Gertsch 1935: 21; Gertsch 1974: 191–192.

*Calileptoneta californica* (Banks): Platnick 1986: 15. Platnick 2002.

**Type material.**—Female holotype, Mt. Diablo, Contra Costa County, California,




Figures 15–23.—*Calileptoneta* species, left chelicerae, female, male. 15. *C. oasa* (Gertsch) from Andreas Canyon. 16. ***C. ubicki*** new species from Arroyo Seco Canyon, arrow to retrodistal cheliceral apophysis. 17. ***C. cokendolpheri*** new species from H. J. Andrews. 18. *C. wapiti* (Gertsch) holotype, arrow to distal tooth. 19. *C. noyoana* (Gertsch), female from Fort Bragg, male holotype, arrow to distal tooth. 20. *C. californica* (Banks), female from Bell Station, male from Mt. Diablo. 21. *C. helferi* (Gertsch), female from Claremont Ave., male holotype. 22. *C. briggsi* new species from Indian Valley Creek Cave. 23. *C. sylva* (Chamberlin & Ivie), female holotype, male from Samwell Cave. Illustrations by JL.

USA, 37°51′N, 121°55′W, June, Fuchs (CASC, lost in 1906 fire).

Male neotype, Mt. Diablo State Park, BBQ/ Wildcat Group Camp, Contra Costa County, California, USA, 37°51′N, 121°55′W, 22 January 2000, J.M. Ledford, under stones (CASC);

**Other material examined.**—USA: *California*: Contra Costa County: Mt. Diablo State Park, BBQ/ Wildcat Group Camp, 37°51′N, 121°55′W, 22 January 2000, J.M. Ledford, under stones (1 ♂, CASC); Napa County: 2 miles W. Oakville, 38°26′N, 122°24′W, 31 Dec. 1953, V. Roth (1 ♂, 1 ♀, AMNH); Santa

Clara County: 9.0 miles N. Bell Station, 37°02′N, 121°18′W, oak grove, under schist, 10 February 1991, D. Ubick (1 ♂, 2 ♀, DU).

**Designation of neotype.**—The holotype of *L. californica* was lost in the California Academy of Sciences during the 1906 earthquake and fire. Many additional specimens have since been collected at the type locality, Mt. Diablo. However, this locality represents an area of sympatry between *C. californica* and *C. helferi* (Fig. 120). *Calileptoneta californica* is by far the rarest of the two species with only two male specimens known from this locality. Gertsch (1974) assigned males with the palpal bulb process reaching the tibia (Figs. 47–52) to *C. californica* and I maintain the association. In order to define this species objectively and clarify its taxonomic status a male from Mt. Diablo conforming to both Banks' (1904) and Gertsch's (1974) description of *C. californica* is designated as a neotype and deposited at the California Academy of Sciences (ICZN 2000, Article 28).

**Diagnosis.**—Distinguished from other *Calileptoneta*, except *C. briggsi*, *C. helferi* and *C. sylva*, by males having a proximal bulb process (Figs. 38–40, 47–49), and a straight retroapical seta (Figs. 39, 48); from *C. briggsi* and *C. sylva* by having the proximal bulb process (Figs. 47–49) elongate, process length 1.0–2.04 × bulb width and having the accessory lobe reduced (Fig. 52); from *C. helferi* by having a shorter palpal tibia, length 0.76–0.90 × carapace width, whereby the proximal bulb process extends the entire length of the tibia, bulb length 1.09–1.40 × tibia length (Figs. 47–49).

**Male (neotype).**—Total length 1.93. Carapace pale yellow-brown with fine dusky mottling surrounding margin, and laterally along caput margins; clypeus with dusky mottling distally; sternum dusky; coxae, trochanters, legs, and pedipalpi with dusky mottling, being especially conspicuous at the bases and apices of the segments.

Carapace 0.80 long, 0.65 wide, height at fovea 0.30 × carapace width; clypeus 0.11 high, chelicerae 0.41 long, fang furrow with 7 teeth along a narrow ridge and 3 denticles on retromargin (Fig. 20). Ocular area 0.20 long, 0.16 wide; diameter PME 0.60 × PLE interdistances. Sternum 0.52 long, 0.47 wide; labium 0.06 long, 0.12 wide; palpal coxae 0.34 long, 0.16 wide.

Spination: palpus: femur p1-2-1-2-2-2, r2-2-2-2-2-1 (apical), patella d1, tibia r3, tarsus r1. Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.64 + 0.26 + 1.81 + 1.51 + 0.97 = [6.19]; II: 1.23 + 0.26 + 1.21 + 1.05 + 0.75 = [4.50]; III: 1.01 + 0.24 + 0.91 + 0.91 + 0.63 = [3.70]; IV: 1.37 + 0.26 + 1.31 + 1.21 + 0.79 = [4.94]; pedipalpus: 0.86 + 0.71 + 0.99 + 0.55 = [3.11]. Femur I 2.52 × carapace width, palpal femur 1.32 × carapace width.

Palpal bulb (Figs. 47–52) 0.69 long, 0.22 wide; palpal tibia with a retroapical group of stiff setae; proximal bulb process (Figs. 47–49) elongate, reaching to base of tibia, bulb length 0.90 × length tibia; embolus narrowly forked at apex; paraembolar setae circular, reaching to base of fork on embolus (Figs. 51, 52); prolateral apical lobe reduced (Fig. 52).

Abdomen dusky with pale chevron pattern, 1.13 long, 0.76 wide.

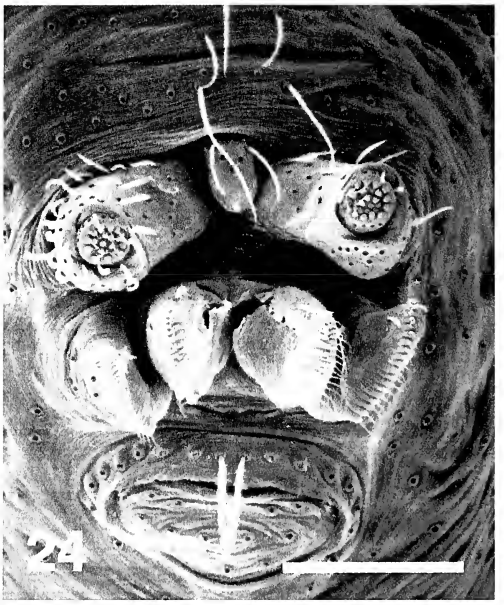
**Variation (*n* = 4).**—Total length 1.86–1.93; carapace length 1.11–1.23 × carapace width; OAL 1.16–1.35 × OAW, diameter PME 0.55–0.64 × PLE interdistances; length femur I 2.24–2.52 × carapace width, palpal femur 1.25–1.42 × carapace width; palpal bulb length 1.09–1.40 × palpal tibia length; proximal bulb process length 1.0–1.54 × bulb width.

**Female (Bell Station).**—Total length 2.31. Coloration and markings same as male.

Carapace 0.91 long, 0.72 wide, height at fovea 0.26 × carapace width; clypeus 0.13 high, chelicerae 0.49 long, fang furrow with 7 teeth on a narrow ridge and 5 denticles on retromargin (Fig. 20). Ocular area 0.20 long, 0.18 wide; diameter PME 0.50 × PLE interdistances. Sternum 0.54 long, 0.54 wide; labium 0.06 long, 0.16 wide; palpal coxae 0.37 long, 0.17 wide.

Spination: palpus: patella d1, tibia r1-1, tarsus p3-1 (apical), r1 (apical), v1 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.76 + 0.32 + 1.96 + 1.58 + 1.05 = [6.67]; II: 1.41 + 0.28 + 1.43 + 1.13 + 0.79 = [5.04]; III: 1.23 + 0.26 + 1.05 + 1.01 + 0.46 = [4.01]; IV: 1.61 + 0.26 + 1.58 + 1.37 + 0.87 = [5.69]; pedipalpus: 0.61 + 0.19 + 0.42 + 1.01 = [2.23]. Femur I 2.44 × carapace width, palpal femur 0.85 × carapace width.

Abdomen 1.40 long, 1.12 wide. Atrium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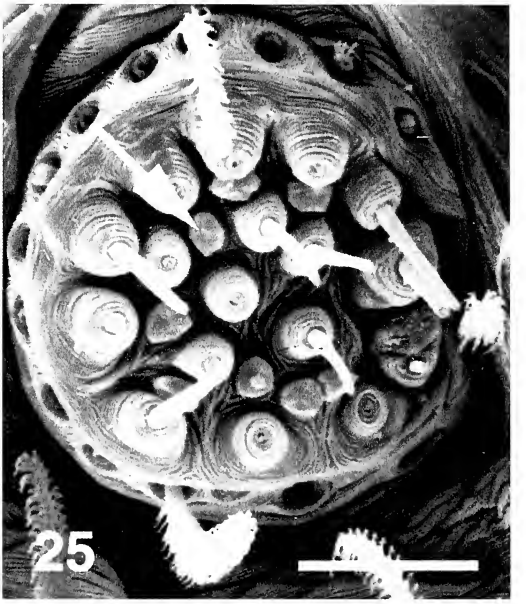
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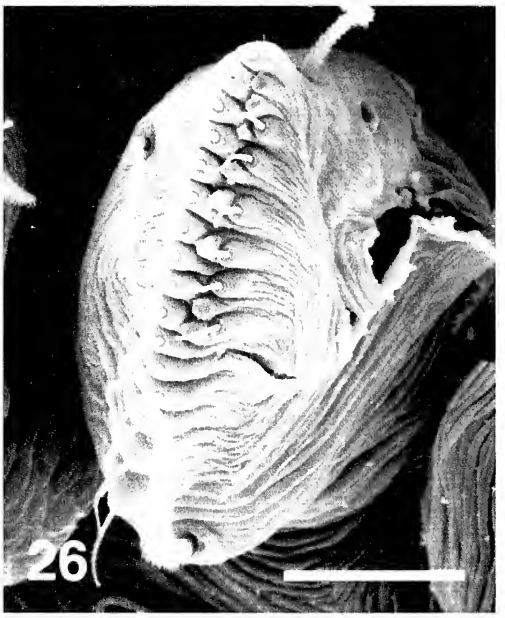
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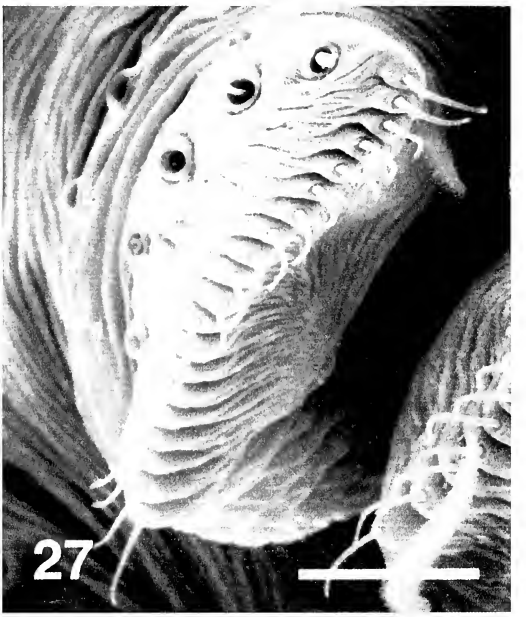
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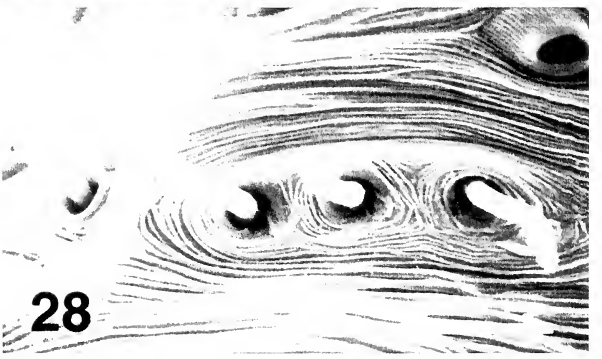
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0.17 long, 0.22 wide, spermathecae 0.73 long (Fig. 113).

**Variation (*n* = 2).**—Total length 2.05–2.31; carapace length 1.26–1.27 × carapace width; OAL 1.11–1.18 × OAW, diameter PME 0.50–0.60 × PLE interdistances; length femur I 2.40–2.44 × carapace width, palpal femur 0.80–0.85 × carapace width; atrium length 0.77–0.83 × width, spermathecae 0.61–0.73 × atrium width (Fig. 114).

**Natural history.**—The Mt. Diablo specimens were found under moist stones in oak woodland sympatrically with *C. helferi*. This species appears to be restricted to drier habitats, unlike *C. helferi*, which also occurs in redwood forest. Interestingly, a single specimen sifted from redwood duff along the Smith River in northern California (Fig. 120) has a palp that conforms to *C. californica*, however, considering its badly damaged condition (almost nothing of the spider remains except the palp), and unknown collector, it is placed as *C. californica* incertae sedis.

**Distribution.**—Central and northwestern California (Fig. 120).

***Calileptoneta cokendolpheri*** new species
Figs. 17, 53–58, 117–118, 121

**Type material.**—Male holotype from pitfall traps in old growth Douglas Fir at the University of Oregon's H. J. Andrews Experimental Forest, Lane County, Oregon, USA, 44°10′N, 122°19′W, June–July 1987, no collector listed (AMNH). Paratypes: USA: *Oregon*: same data as holotype (6 ♂, 3 ♀, AMNH).

**Etymology.**—This species is named in honor of Mr. James Cokendolpher, who contributed additional leptonetid specimens to this study and shared insights into the oftentimes difficult morphology of these spiders.

**Diagnosis.**—Males are distinguished from all other *Calileptoneta* species by having 2 proapical flanges (Fig. 57), with the basal flange bearing numerous setae, and the apical flange being tightly curled. *Calileptoneta cokendolpheri* may be further distinguished from other *Calileptoneta*, except *C. oasa* and *C. ubicki*, by lacking a proximal bulb process (Figs. 32–34) and the retroapical pair of twisted palpal tarsal setae; and from *C. oasa* and *C. ubicki* by having a hook-shaped embolus (Fig. 56).

**Male (holotype).**—Total length 2.33. Specimen pale. Carapace and all leg segments, including pedipalps, dark yellow-brown.

Carapace 1.10 long, 0.91 wide, height at fovea 0.50 × carapace width; clypeus 0.19 high, chelicerae 0.93 long, fang furrow with 9 teeth along a narrow ridge and 4 denticles on retromargin (Fig. 17). Ocular area 0.15 long, 0.19 wide; diameter PME 0.64 × PLE interdistances. Sternum 0.60 long, 0.65 wide; labium 0.11 long, 0.18 wide; palpal coxae 0.52 long, 0.22 wide.

Spination: palpus: patella d1, tibia r1-1-1-1-2 (apical), tarsus r1 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.88 + 0.32 + missing + missing + missing = [N/A]; II: 1.46 + 0.29 + 1.51 + 1.34 + 0.85 = [5.45]; III: 1.24 + 0.29 + 1.24 + 1.15 + 0.78 = [4.70]; IV: 1.63 + 0.29 + missing + missing + missing = [N/A]; pedipalpus: 0.54 + 0.23 + 0.29 + 0.35 = [1.41]. Femur I 2.07 × carapace width, palpal femur 0.59 × carapace width.

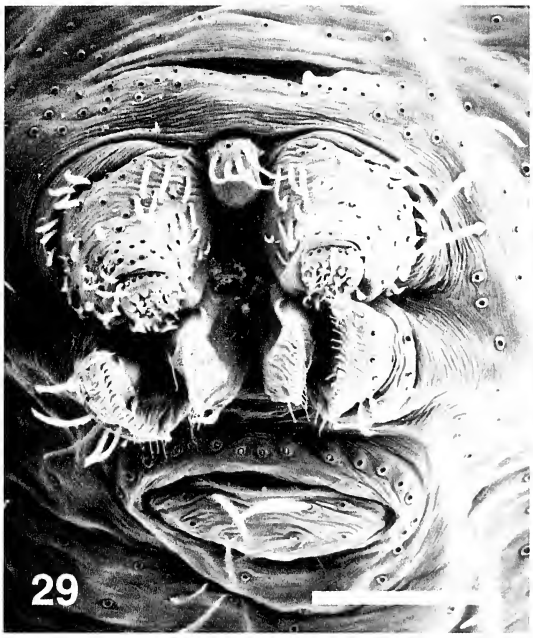
Palpal bulb (Figs. 53–58) 0.42 long, 0.23 wide; palpal tibia with a retroapical group of stiff setae; embolus hook-shaped (Fig. 56); paraembolar setae fan-like, with a single seta extending to base of hook on embolus (Fig. 56); ventral ridge bearing 2 proapical flanges (Fig. 57), with the basal flange bearing numerous setae, and the apical flange being tightly curled; prolateral apical lobe reduced (Fig. 58).

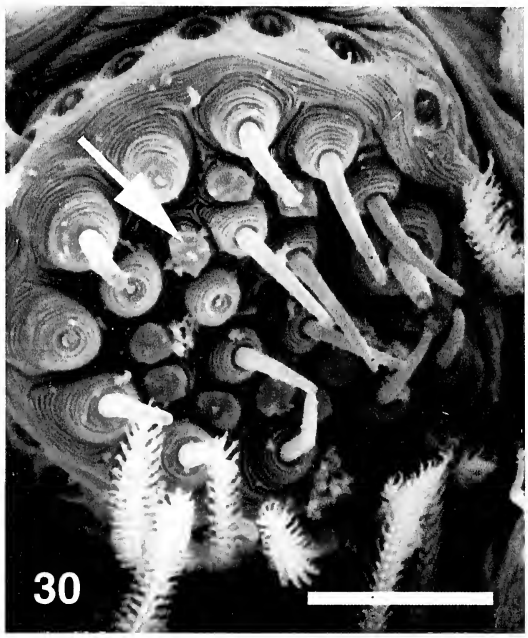
Abdomen dark, without chevron pattern, 1.23 long, 1.07 wide.

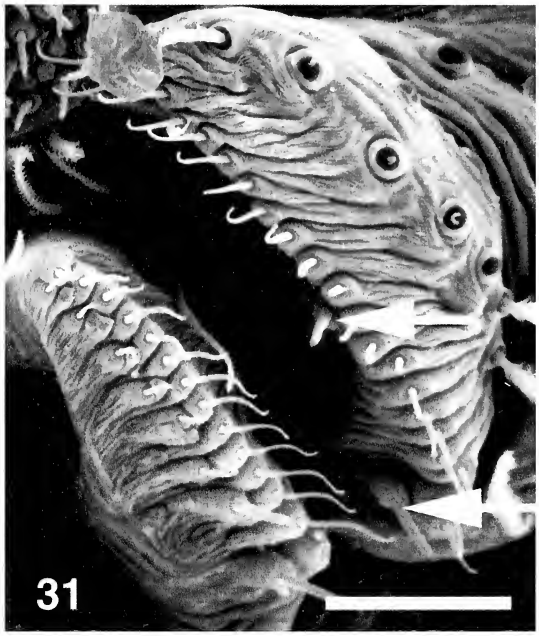
**Variation (*n* = 2).**—Total length 2.14–2.33; carapace length 1.20–1.22 × carapace width; OAL 0.78–1.22 × OAW, diameter PME 0.64 × PLE interdistances; length femur I 2.07–2.15 × carapace width, palpal femur 0.59–0.76 × carapace width; palpal bulb length 1.30–1.46 × palpal tibia length.

←

Figures 24–28.—*Calileptoneta helferi* (Gertsch), male from Mt. Diablo, spinning organs. 24. Ventral. 25. Left ALS, arrow to tartipore. 26. Right PMS. 27. Right PLS. 28. Epiandrous spigots. Scale bars: A = 120 μm, B = 13.6 μm, C = 27 μm, D = 25 μm.



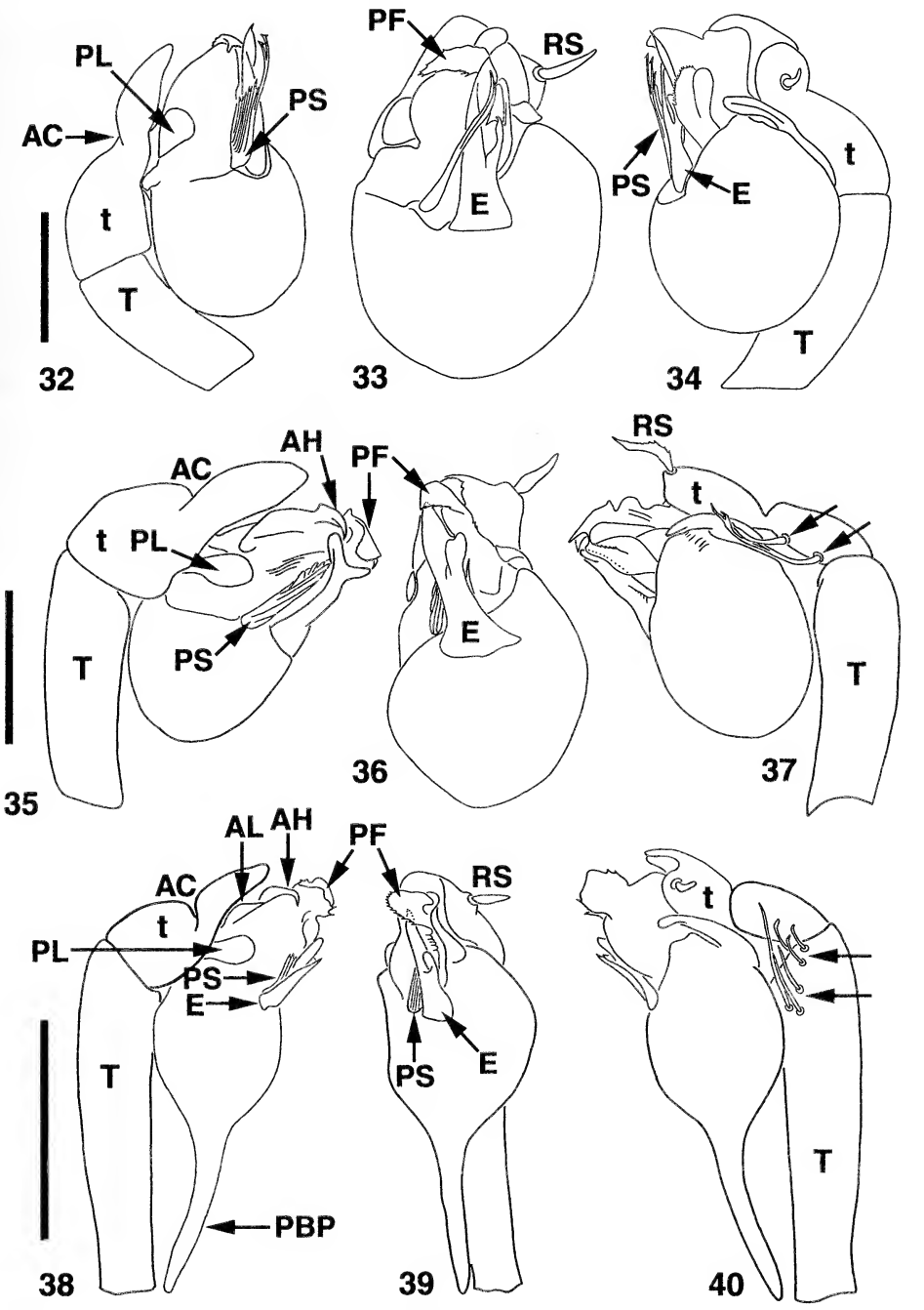




Figures 29–31.—*Calileptoneta* sp., female from Mt. Diablo, spinning organs. 29. Ventral. 30. Left ALS, arrow to tartipore. 31. Left PLS, PMS, arrows to cylindrical gland spigots. Scale bars: A = 120 μm, B = 13.6 μm, C = 30 μm.

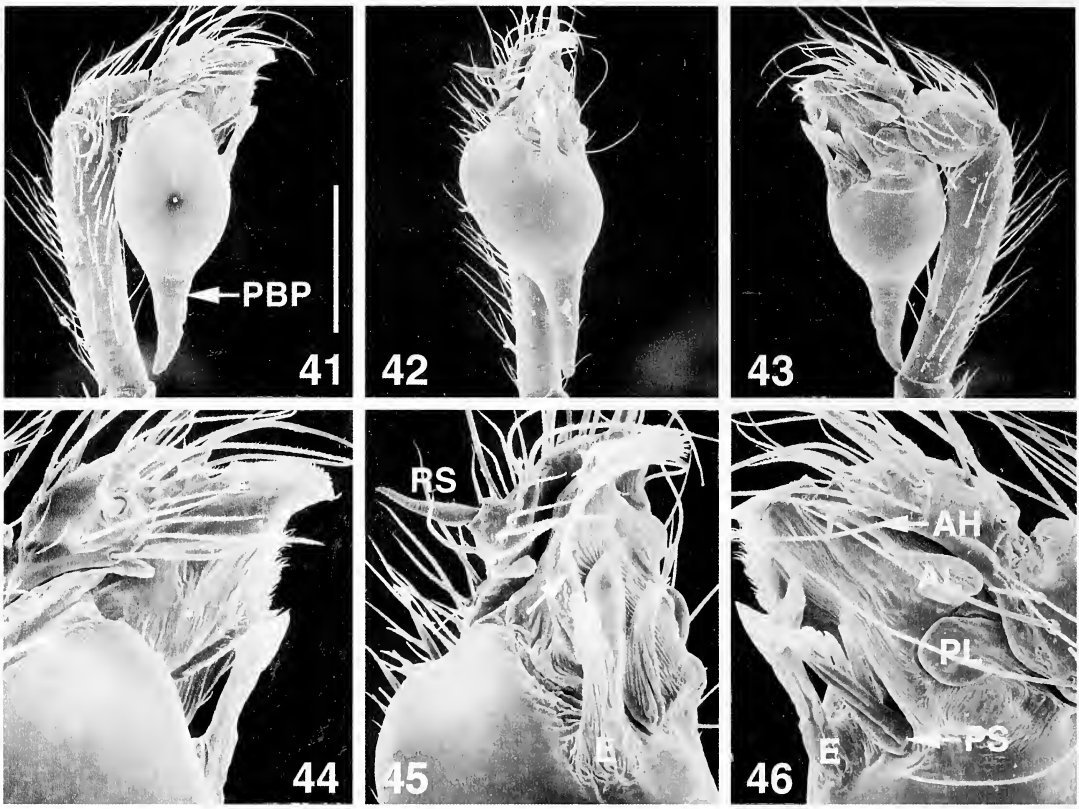
**Female (paratype).**—Total length 2.47. Coloration and markings same as male.

Carapace 1.0 long, 1.0 wide, height at fovea 0.45 × carapace width; clypeus 0.19 high, chelicerae 0.58 long, fang furrow with 9 teeth along a narrow ridge and 5 denticles on retromargin (Fig. 17). Ocular area 0.21 long, 0.19 wide; diameter PME 0.50 × PLE interdistances. Sternum 0.62 long, 0.65 wide; labium 0.09 long, 0.17 wide; palpal coxae 0.51 long, 0.21 wide.

Spination: palpus: patella d1, tibia v1-2, tarsus p 1(apical), r1 (apical), v 1(apical). Leg measurements (Femur + Patella + Tibia +




Figures 32–40.—*Calileptoneta* sp., male genitalia, left palpus. 32–34. *C. oasa*, Andreas Canyon. 35–37 *C. wapiti*, Cameron Road, arrows on 37 to retroapical tibial setae. 38–40. *C. californica* Mt. Diablo, arrows on 40 to retroapical setae. AC = apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PBP = proximal bulb process, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical tarsal seta, T = tibia, t = tarsus. Scale bars: 32–34 = 0.20 mm, 35–37 = 0.20 mm, 38–40 = 0.40 mm. Illustrations by JL.




Figures 41–46.—*Calileptoneta briggsi* new species, male from Indian Valley Creek Cave, right palpus. 41. retrolateral. 42. ventral. 43. prolateral. 44. retrolateral. 45. ventral. 46. prolateral. AC = apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PBP = proximal bulb process, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 41–43= 250 μm, 44–46 = 100 μm.

Metatarsus + Tarsus = [Total]): I: 1.78 + 0.32 + missing + missing + missing = [N/A]; II: 1.46 + 0.27 + 1.46 + 1.15 + 0.80 = [5.14]; III: 1.27 + 0.24 + missing + missing + missing = [N/A]; IV: 1.54 + 0.24 + 1.32 + 1.29 + missing = [N/A]; pedipalpus: 0.53 + 0.20 + 0.40 + 0.59 = [1.72]. Femur I 1.78 × carapace width, palpal femur 0.53 × carapace width.

Abdomen 1.47 long, 0.96 wide. Atrium 0.18 long, 0.25 wide, spermathecae 0.17 long (Fig. 117).

**Variation (*n* = 2).**—Total length 2.44–2.47; carapace length 1.0–1.27 × carapace width; OAL 1.0–1.10 × OAW, diameter PME 0.50 × PLE interdistances; length femur I 1.54–1.78 × carapace width, palpal femur 0.51–0.53 × carapace width; atrium length 0.72–0.81 × width, spermathecae 0.68–0.69 × atrium width (Fig. 118).

**Natural history.**—The entire series of specimens representing this species were collected in old growth Douglas Fir (*Pseudotsuga menziesii*) using pitfall traps.

**Distribution.**—Known only from the type locality (Fig. 121).

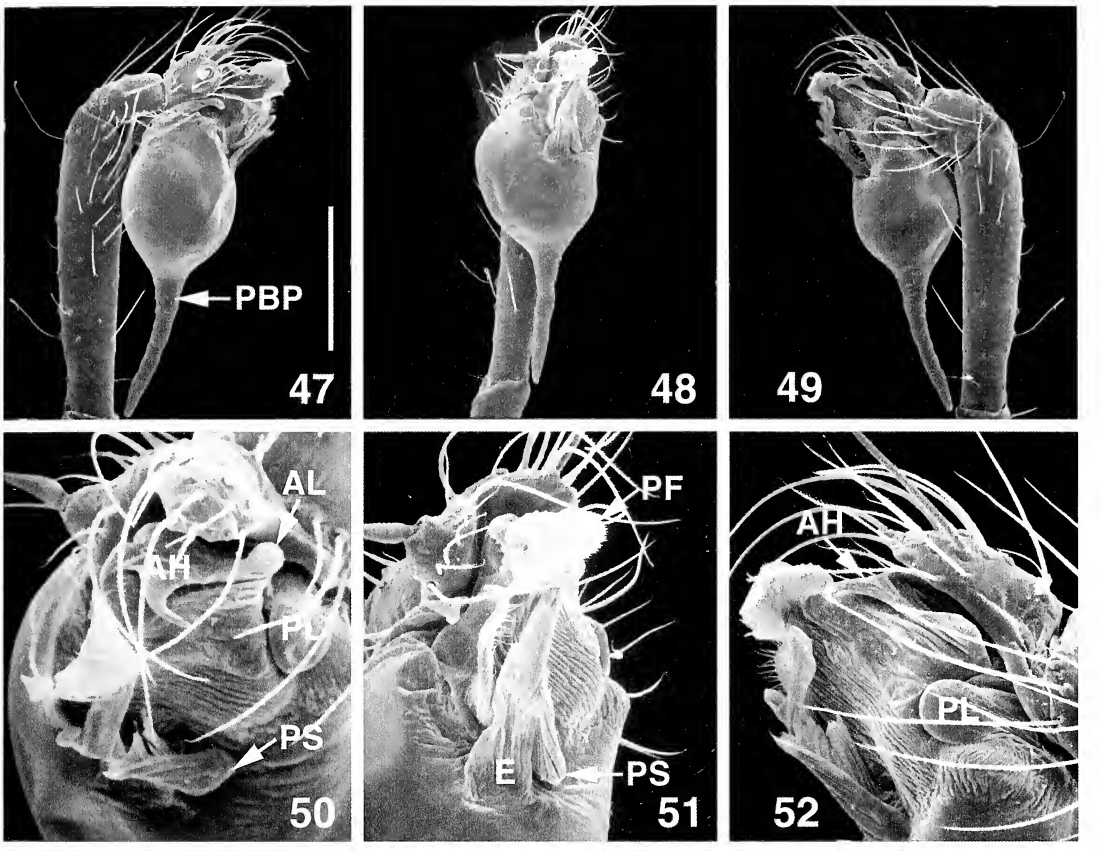
*Calileptoneta helferi* (Gertsch 1974)
Figs. 6, 7, 21, 24–28, 59–64, 115–116, 120

*Leptoneta helferi* Gertsch 1974: 192–194; Brignoli 1977: 217.

*Calileptoneta helferi* (Gertsch): Platnick 1986: 15; Platnick 2002.

**Type material.**—Male holotype, Carlotta, Humboldt County, California, USA, 40°32′N, 124°03′W, 15 September 1961, W. Ivie, W.J. Gertsch (AMNH, examined).

**Other material examined.**—USA: *California*: Alameda County: Claremont Ave, 2.2 miles above Berkeley RB-2, 37°52′N, 122°16′W, 10 May 1963, P.R. Craig, D. Dailey (1 ♀, 1 ♂, CASC); Contra Costa County: Mt.



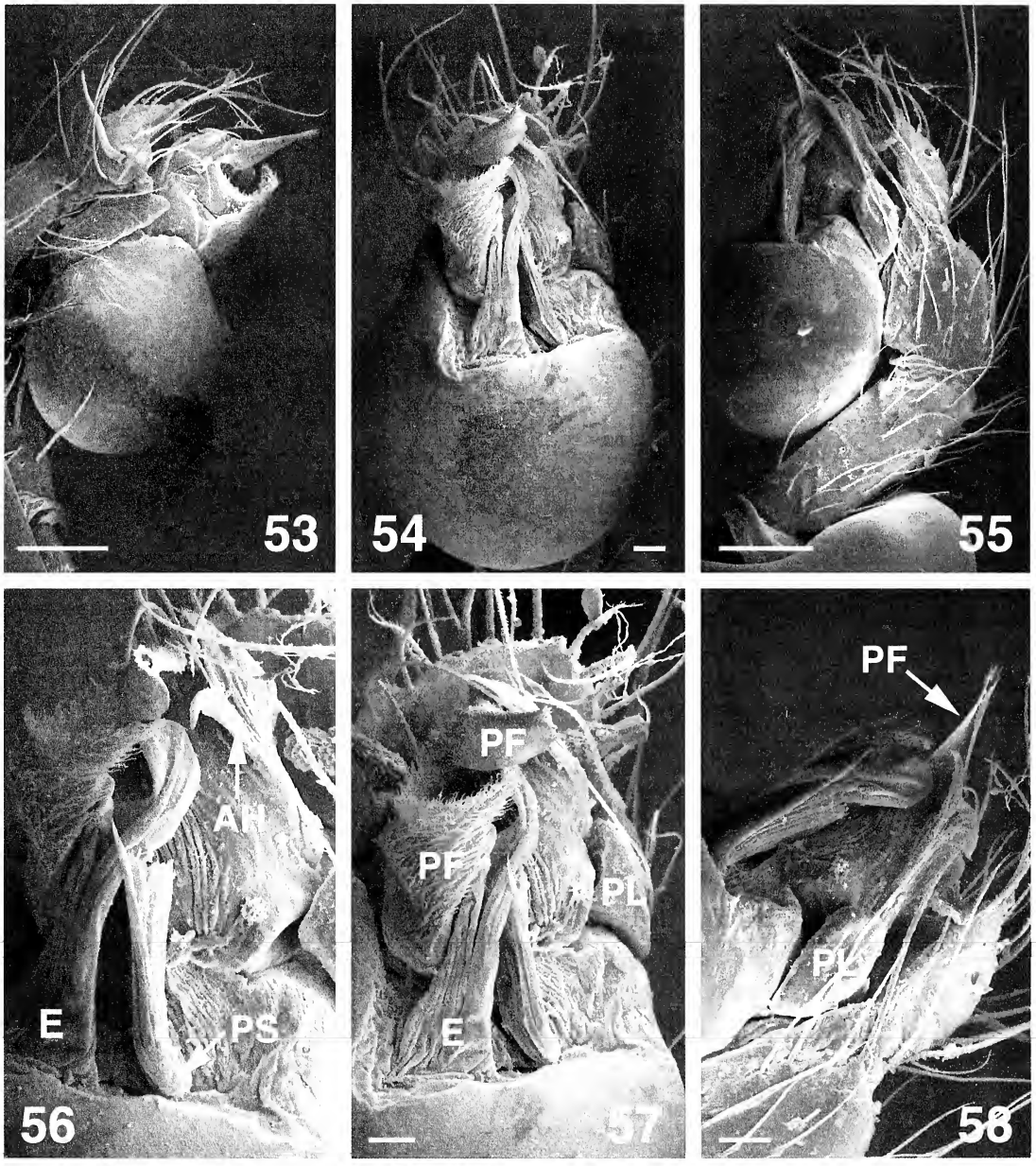

Figures 47–52.—*Calileptoneta californica* (Banks), male from Mt. Diablo, right palpus. 47. retrolateral. 48. ventral. 49. prolateral. 50. ventroapical. 51. ventral. 52. prolateral. AC = apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PBP = proximal bulb process, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 47 = 150 μm, 48–49 = 231 μm, 50 = 75 μm, 51–52 = 86 μm.

Diablo State Park, BBQ/ Wildcat Group Camp, 37°51′N, 121°55′W, 22 January 2000, J.M. Ledford, under stones (4 ♂, 3 ♀, CASC), 6 February 2000, J.M. & K.E. Ledford, under stones (3 ♂, 2 ♀, CASC); Humboldt County: F.K. Lane State Park., nr. Phillipsville, 40°12′N, 123°47′W, 1 Oct 1959, V. Roth (1 ♂, AMNH); Mendocino County: Fault Rock Cave, 2 January 1960, R.E. Graham (#1622, 2 juveniles; #1623, 2 ♀; #1625, 2 ♂, 2 ♀, AMNH); 4.2 miles S. Piercy, 39°57′N, 123°47′W, 17 February 1967, V. Roth (1 ♂, AMNH); Yolo County: 18.5 km ESE Lower Lake, 38°52′N, 122°23′W, 14. v-7–1993, B.L. Fisher, pitfall traps, non-serpentine, chaparral (1 ♂, CASC).

**Diagnosis.**—Distinguished from other *Calileptoneta*, except *C. briggsi*, *C. californica*, and *C. sylva*, by males having a proximal bulb process (Figs. 38–40, 59–61), and a straight retroapical seta (Fig. 39); from *C. briggsi* and *C. sylva* by having the proximal bulb process (Figs. 59–61) elongate, process length 1.0–2.04 × bulb width, and having the accessory lobe reduced (Fig. 64); from *C. californica* by having an elongate palpal tibia, length 1.02–1.19 × carapace width, whereby the proximal bulb process does not reach the base of the tibia, bulb length 0.81–1.04 × tibia length.

**Male (holotype).**—Total length 2.29. Coloration and markings same as for *C. californica*, except considerably darker throughout.

Carapace 1.13 long, 0.93 wide, height at fovea 0.39 × carapace width; clypeus 0.17 high, chelicerae 0.71 long, fang furrow with 5 teeth along a narrow ridge and 5 denticles on retromargin (Fig. 21). Ocular area 0.30 long, 0.23 wide; diameter PME 0.75 × PLE interdist-

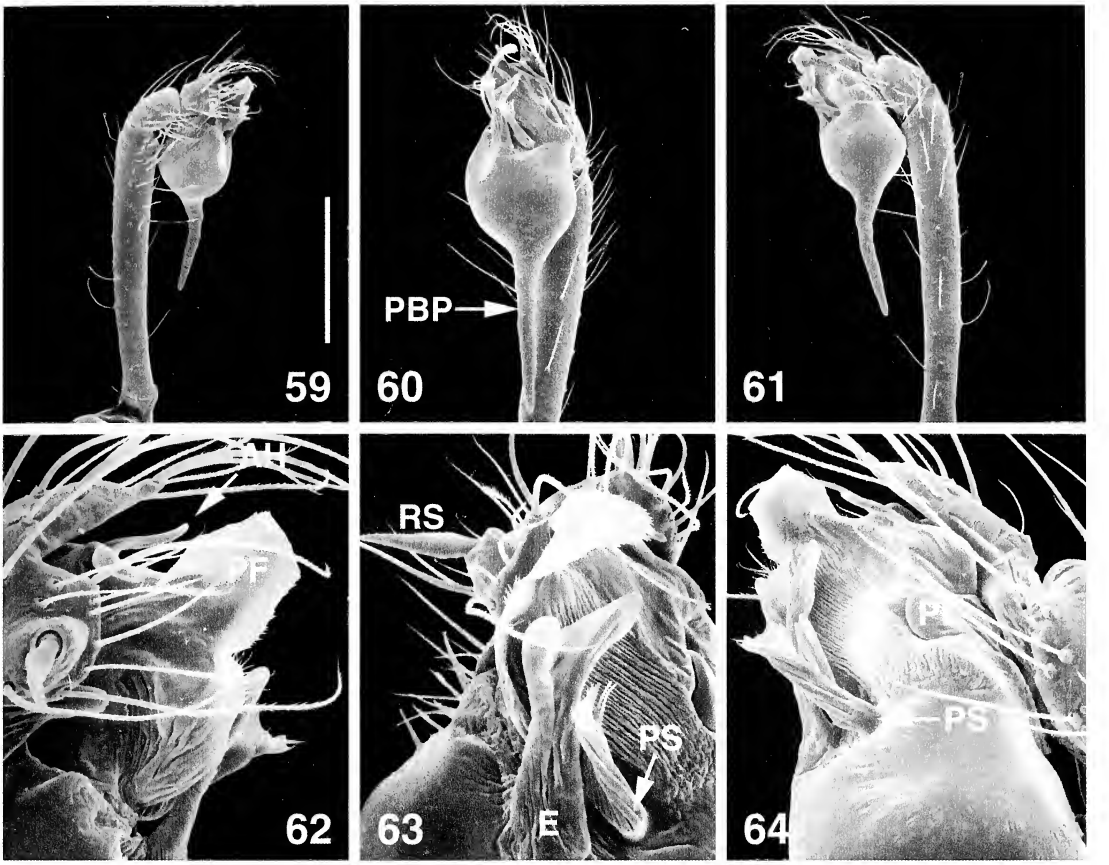



Figures 53–58.—*Calileptoneta cokendolpheri* new species, male from H. J. Andrews, right palpus. 53. retrolateral. 54. ventral. 55. prolateral. 56. retroventral. 57. ventral. 58. proapical. AH = apical hook, E = embolus, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae. Scale bars: 53 = 100 μm, 54 = 20 μm, 55 = 100 μm, 56–58 = 30 μm.

ances. Sternum 0.67 long, 0.70 wide; labium 0.08 long, 0.15 wide; palpal coxae 0.55 long, 0.21 wide.

Spination: palpus: femur p2-1-2-3-3-2-3-3-2-3-3, r1-1-2-1-1-1-2-1-2-2-2-2-2-1-1, v1 (apical); patella d1, tibia r2, tarsus r1. Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 2.16 + 0.34 + 1.90 + 1.60 + 1.00 = [7.00]; II: 1.74 + 0.32 + 1.77 + 1.43 + 0.95 = [6.21]; III: 1.47 + 0.30 + 1.31 + 1.25 + 0.83 = [5.16]; IV: 1.86 + 0.30 + 1.86 + 1.60 + 1.00 = [6.62]; pedipalpus: 1.53 + 0.64 + 1.02 + 0.36 = [3.55]. Femur I 2.32 × carapace width, palpal femur 1.65 × carapace width.

Palpal bulb (Figs. 59–64) 1.0 long, 0.25




Figures 59–64.—*Calileptoneta helferi* (Gertsch), male from Mt. Diablo, right palpus. 59. retrolateral. 60. ventral. 61. prolateral. 62. retrolateral. 63. ventral. 64. prolateral. AC= apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PBP = proximal bulb process, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 59 = 300 μm, 60 = 231 μm, 61 = 300 μm, 62 = 43 μm, 63 = 75 μm, 64 = 86 μm.

wide; palpal tibia with a retroapical group of stiff setae; proximal bulb process elongate, not reaching to base of tibia, bulb length 0.98 × length tibia; embolus narrowly forked at apex; paraembolar setae circular, reaching to base of fork on embolus (Figs. 63, 64); prolateral apical lobe reduced (Fig. 64).

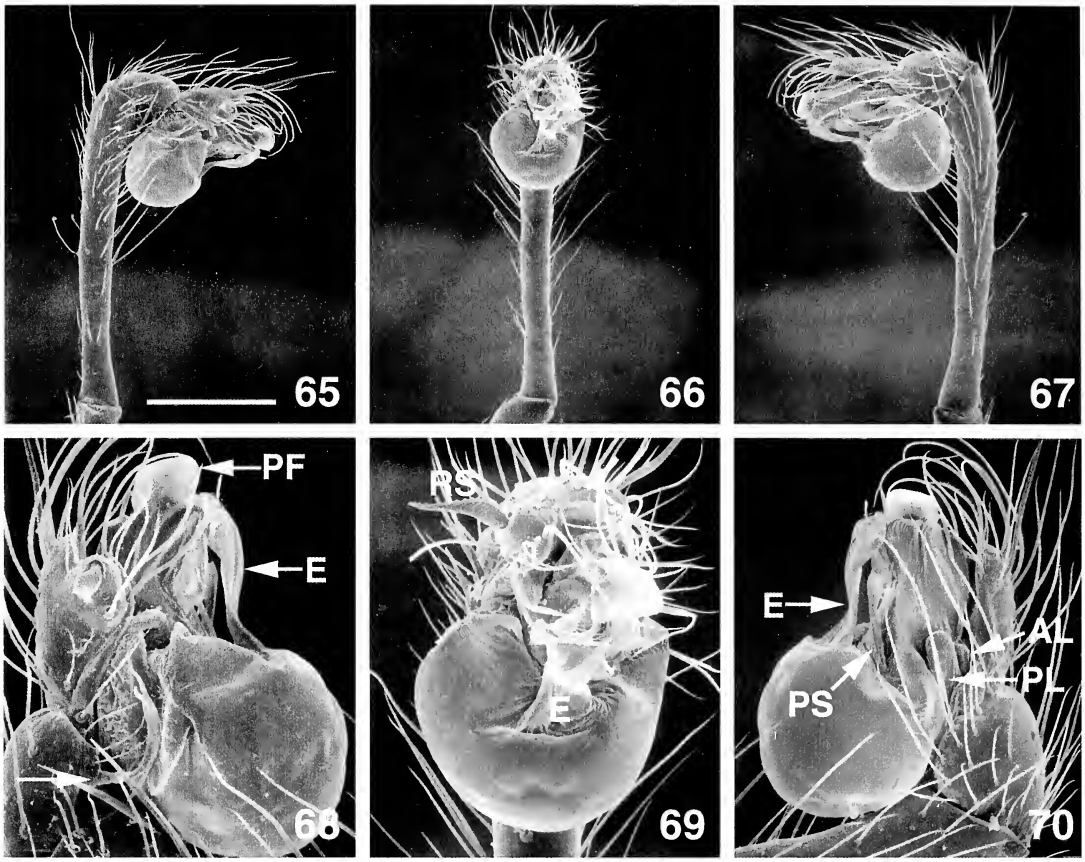
Abdomen dusky with pale chevron pattern (Fig. 6), 1.16 long, 1.05 wide.

**Variation (*n* = 9).**—Total length 2.04–2.34; carapace length 1.15–1.29 × carapace width; OAL 1.14–1.45 × OAW, diameter PME 0.50–0.73 × PLE interdistances; length femur I 2.15–2.66 × carapace width, palpal femur 1.34–1.98 × carapace width; palpal bulb length 0.81–1.10 × palpal tibia length; proximal bulb process length 1.40–2.04 × bulb width.

**Female (Claremont Ave.).**—Total length 2.25. Coloration and markings same as male.

Carapace 0.92 long, 0.73 wide, height at fovea 0.26 × carapace width; clypeus 0.12 high, chelicerae 0.45 long, fang furrow with 7 teeth on a narrow ridge and 3 denticles on retromargin (Fig. 21). Ocular area 0.25 long, 0.22 wide; diameter PME 0.50 × PLE interdistances. Sternum 0.57 long, 0.51 wide; labium 0.08 long, 0.15 wide; palpal coxae 0.36 long, 0.18 wide.

Spination: palpus: patella d1, tarsus p2-1-1, r1-1, v1-2 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.47 + 0.30 + 1.62 + 0.95 + 0.87 = [5.21]; II: 1.23 + 0.28 + 1.11 + 0.97 + 0.71 = [4.30]; III: 1.03 + 0.28 + 0.95 + 0.85 + 0.61 = [3.72]; IV: 1.37 + 0.26 + 1.25 +




Figures 65–70.—*Calileptoneta noyoana* (Gertsch), male from Fort Bragg, right palpus. Arrow on 68 to retroapical setae. 65. retrolateral. 66. ventral. 67. prolateral. 68. retrolateral. 69. ventroapical. 70. retrolateral. AC = apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 65–67 = 200 μm, 68–70 = 75 μm.

1.09 + 0.75 = [4.72]; pedipalpus: 0.54 + 0.17 + 0.39 + 0.49 = [1.59]. Femur I 2.01 × carapace width, palpal femur 0.74 × carapace width.

Abdomen 1.33 long, 1.06 wide. Atrium 0.14 long, 0.19 wide, spermathecae 0.13 long (Fig. 115).

**Variation (*n* = 3).**—Total length 2.24–2.40; carapace length 1.21–1.26 × carapace width; OAL 1.14–1.19 × OAW, diameter PME 0.50–0.64 × PLE interdistances; length femur I 2.01–2.13 × carapace width, palpal femur 0.74–0.80 × carapace width; atrium length 0.74–0.81 × width, spermathecae 0.68–1.18 × atrium width.

**Natural history.**—The Mt. Diablo specimens were found under moist stones in oak woodland sympatrically with *C. californica*.

**Distribution.**—Northwestern California (Fig. 120).

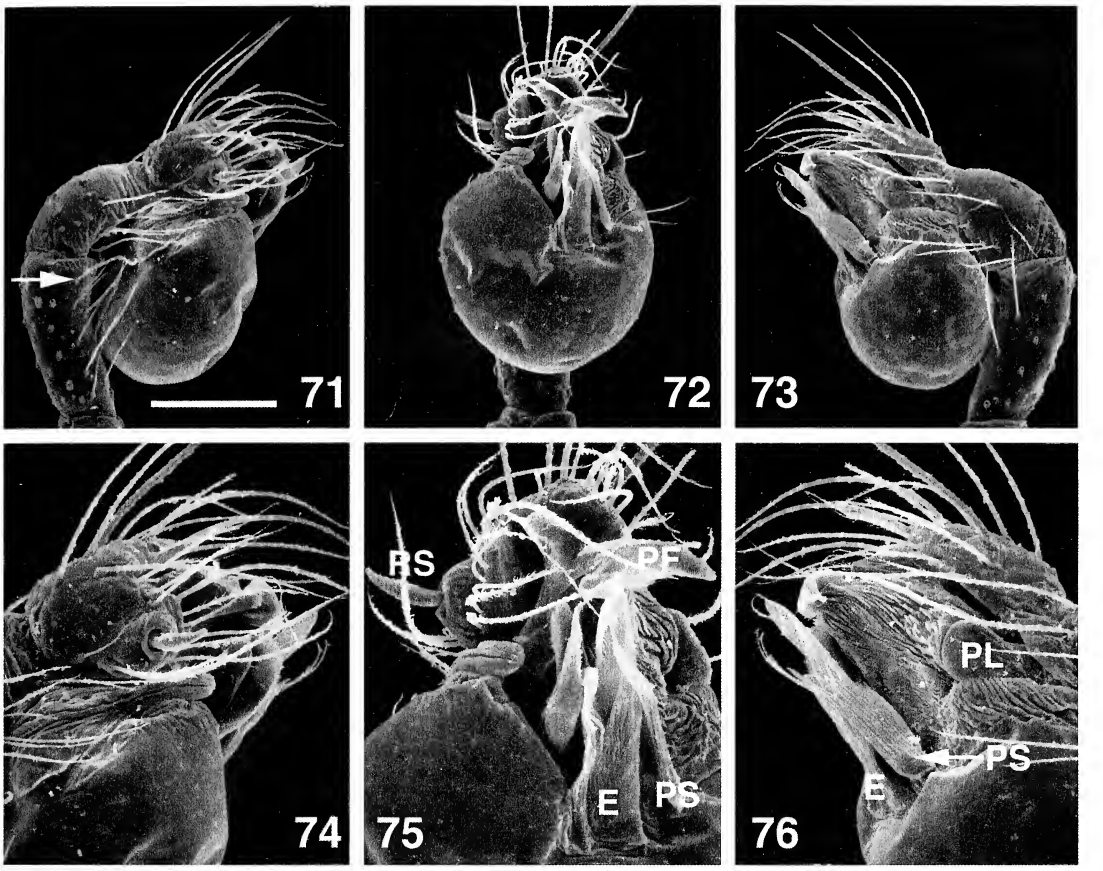
*Calileptoneta noyoana* (Gertsch 1974)
Figs. 4–5, 19, 65–70, 96, 100–101, 106–108, 120

*Leptoneta noyoana* Gertsch 1974: 196–197; Brignoli 1977: 217.

*Calileptoneta noyoana* (Gertsch): Platnick 1986: 15; Platnick 2002.

**Type material.**—Male holotype from 12–15 miles E. Noyo, Mendocino County, California, USA, 39°25′N, 123°48′W, 13 September 1961, W.J. Gertsch, W. Ivie (AMNH, examined)

**Material examined.**—USA: *California*: Humboldt County: Humboldt Redwoods State Park, Founder's Grove, 40°21′N, 123°55′W,

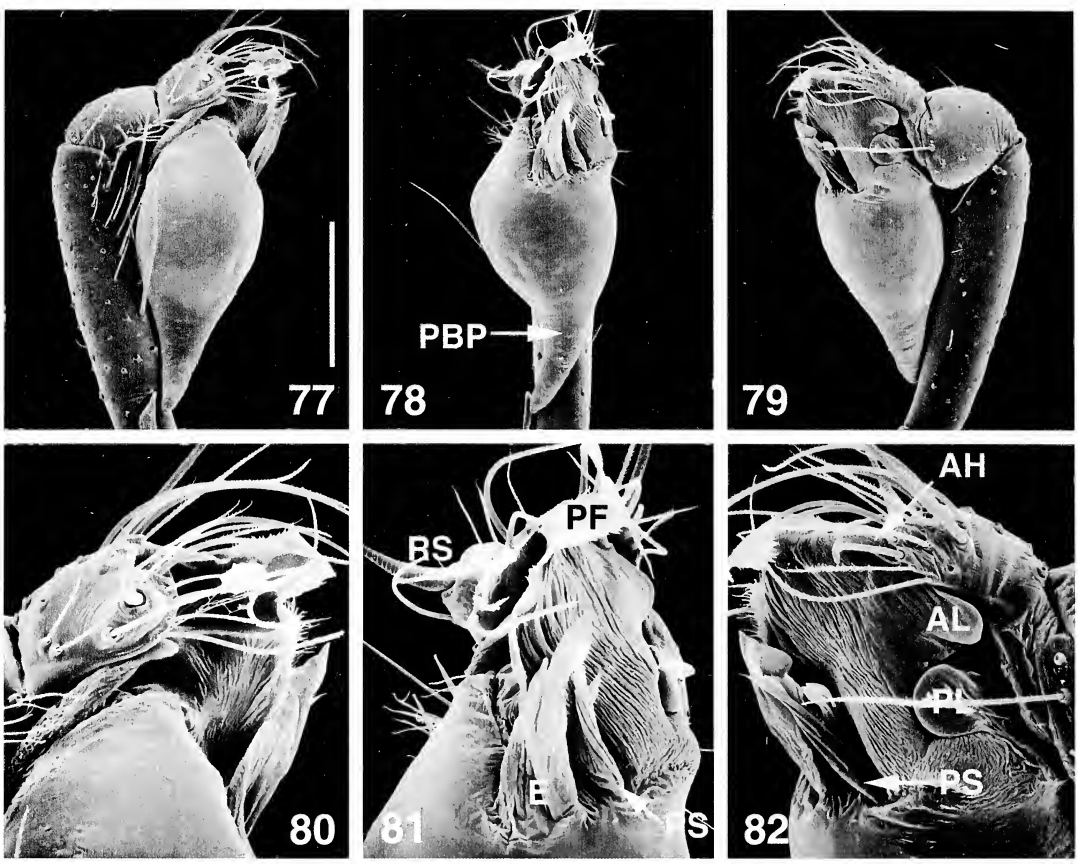



Figures 71–76.—*Calileptoneta oasa* (Gertsch), male from Andreas Canyon, right palpus. 71. retrolateral. 72. ventral. 73. prolateral. 74. retroapical. 75. ventroapical. 76. proapical. AC = apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 71–73 = 136 μm, 74–76 = 75 μm.

28 October 1990, in redwood duff, D. Ubick, W. Rauscher (2 ♀, 2 juveniles including penultimate male, DU); Humboldt Redwoods State Park, Tall Tree, 40°19′N, 123°59′W, 250 ft. elevation, 11 September 1992, D. Ubick, J. Boutin (3 ♀, 2 juveniles including penultimate male, DU); Mendocino County: Jackson State Forest, Camp Dunlap Area, 39°21′N, 123°33′W, 16 September 1990, in redwood duff, D. Ubick (1 ♂, DU); 0.5 miles W. Camp Dunlap, 39°21′N, 123°33′W, 400 ft. elevation, 16 September 1990, in redwood duff, D. Ubick (1 ♀, DU); Dunlap Camp, 39°21′N, 123°33′W, 400 ft. elevation, 7 September 1992, in redwood duff, D. Ubick, J. Boutin (1 ♀, DU); 3.0 miles S. Rockport, 39°44′N, 123°48′W, 300 ft. elevation, 19 September 1990, in redwood duff, D. Ubick (1 ♂, DU); 2.0 miles S. Usal Campground, 39°50′N, 123°50′W, 1000 ft. elevation, 19 September 1990, in redwood duff, D. Ubick (1 ♀, DU); 1 miles NE Usal Road along HWY 1, 200 ft. elevation, 39°50′N, 123°50′W, 20 September 1990, D. Ubick (1 ♂, DU); Big River Camp, ~2 miles W. James Creek, 39°20′N, 123°30′W, 5 May 1991, in redwood duff, D. Ubick (2 ♂, 2 ♀, 3 juveniles, DU); Noyo River, 14.5 air miles E. Fort Bragg, 39°25.5′N, 123°32′W, 25–26.v.1996, C.E. Griswold (2 ♂, 1 ♀, juvenile, CASC).

**Diagnosis.**—Distinguished from other *Calileptoneta*, except *C. wapiti*, by having males with retrolateral twisted tarsal setae on the palpus (Figs. 37, 68) and an enlarged distal cheliceral tooth (Fig. 19); from *C. wapiti* by having an elongate palpal femur, 2.24–2.78 × carapace width (Fig. 5).

**Male (holotype).**—Total length 2.26. Spec-




Figures 77–82.—*Calileptoneta sylva* (Chamberlin & Ivie), male from Samwell Cave, right palpus. 77. retrolateral. 78. ventral. 79. prolateral. 80. retroapical. 81. ventroapical. 82. retroapical. AC = apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PBP = proximal bulb process, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 77–79 = 200 μm, 80–82 = 86 μm.

imen faded. Carapace yellow-brown with dusky mottling along margin; clypeus yellow-brown; sternum yellow-brown; coxae, trochanters, legs, and pedipalpi with dusky mottling, being especially conspicuous at the bases and apices of the segments.

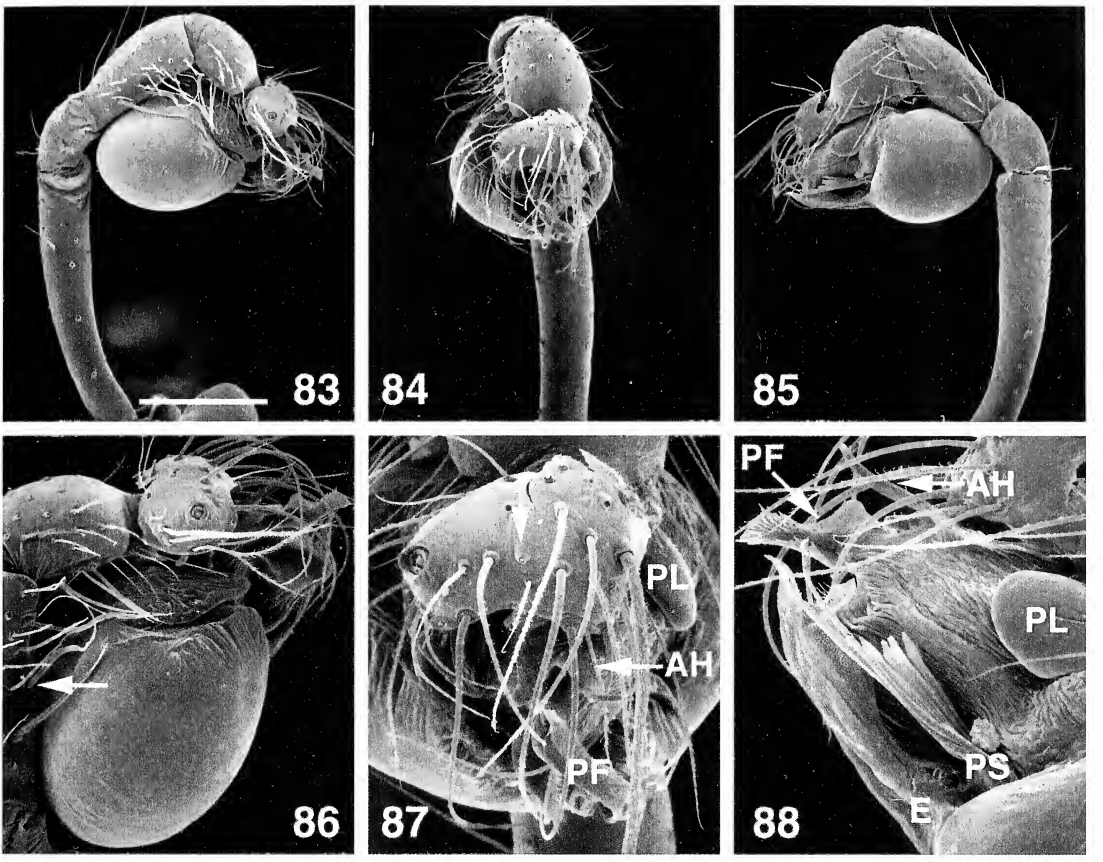
Carapace 1.06 long, 0.87 wide, height at fovea 0.46 × carapace width; clypeus 0.15 high, chelicerae 0.74 long, fang furrow with 8 teeth along a narrow ridge and 5 denticles on retromargin (Fig. 19). Ocular area 0.30 long, 0.22 wide; diameter PME 0.70 × PLE interdistances. Sternum 0.63 long, 0.58 wide; labium 0.10 long, 0.18 wide; palpal coxae 0.50 long, 0.24 wide.

Spination: palpus: patella d1, tibia r3-1-1, tarsus p1(apical), r1-1-1 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 2.04 + 0.34 + 2.17 + 1.70 + 1.02 = [7.27]; II: 1.56 + 0.32 + 1.60 + 1.34 + 0.93 = [5.74]; III: 1.29 + 0.24 + 1.24 + 1.15 + 0.73 = [4.65]; IV: 1.73 + 0.29 + 1.70 + 1.44 + 0.90 = [6.06]; pedipalpus: 2.42 + 1.31 + 1.21 + 0.46 = [5.40]. Femur I 2.34 × carapace width, palpal femur 2.78 × carapace width.

Palpal bulb (Figs. 65–70) 0.49 long, 0.27 wide; retroapical seta proximally broad and tapering to a point distally; embolus broadly forked at apex; paraembolar setae fan-like, with 3 truncate setae at the base, and a single seta forming a broad flange distally; accessory lobe reduced (Fig. 70).

Abdomen dusky with pale chevron pattern (Fig. 4), 1.20 long, 0.96 wide.

**Variation ($n$ = 4).**—Total length 2.17–2.50; carapace length 1.21–1.59 × carapace width; OAL 1.20–1.37 × OAW, diameter PME 0.60–




Figures 83–88.—*Calileptoneta ubicki* new species, male from Arroyo Seco Canyon, right palpus. 83. retrolateral. 84. ventral. 85. prolateral. 86. retrolateral. 87. ventroapical. 88. proapical. AC = apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 83 = 250 μm, 84 = 231 μm, 85 = 270 μm, 86 = 136 μm, 87 = 86 μm, 88 = 75 μm.

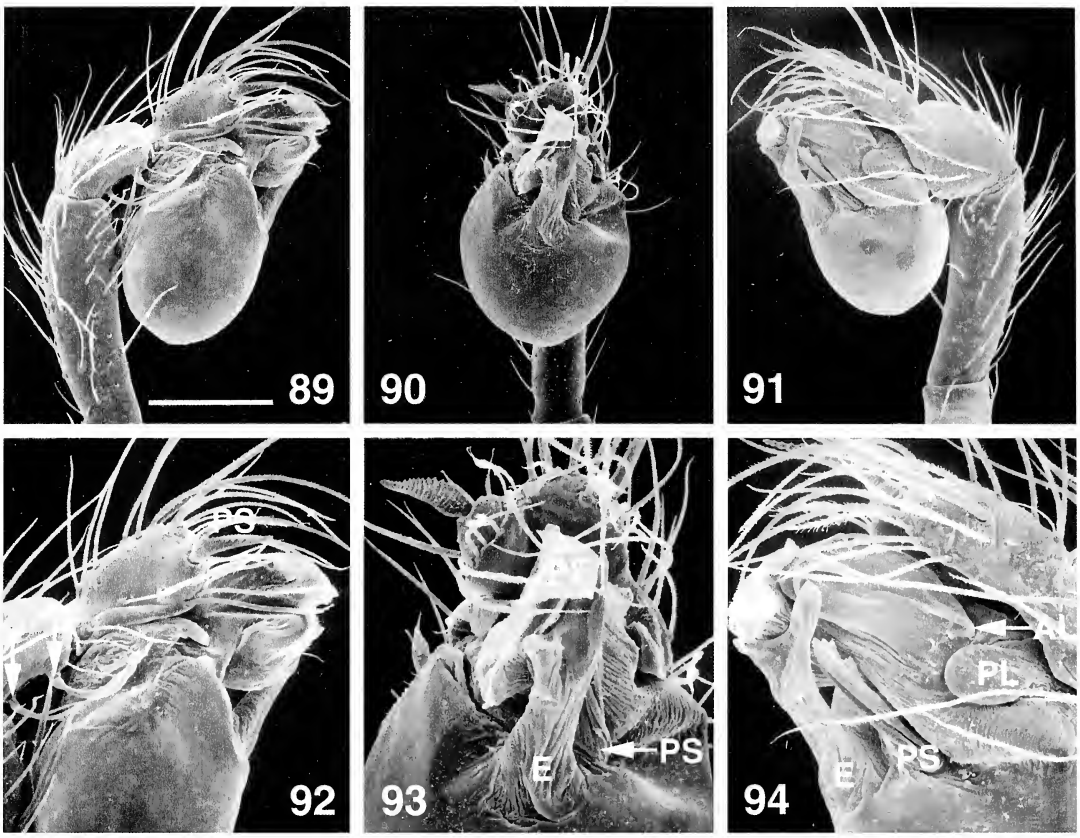
0.70 × PLE interdistances; length femur I 2.32–2.35 × carapace width, palpal femur 2.24–2.78 × carapace width; bulb length 0.40–0.45 × palpal tibia length; abdomen pale to dusky, with or without chevron pattern.

**Female (Fort Bragg).**—Total length 2.24. Coloration and markings same as male. Carapace 0.69 long, 0.59 wide, height at fovea 0.50 × carapace width; clypeus 0.11 high, chelicerae 0.33 long, fang furrow with 8 teeth along a narrow ridge and 3 denticles on retromargin (Fig. 19). Ocular area 0.24 long, 0.19 wide; diameter PME 0.50 × PLE interdistances. Sternum 0.54 long, 0.56 wide; labium 0.09 long, 0.16 wide; palpal coxae 0.36 long, 0.20 wide.

Spination: palpus: patella d1, tarsus p2-1-1 (apical), r1-1 (apical). Leg Measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.41 + 0.29 + 1.54 + 1.15 + 0.85 = [5.24]; II: 1.17 + 0.29 + 1.20 + 0.93 + 0.73 = [4.32]; III: 1.04 + 0.24 + 0.90 + 0.83 + 0.61 = [4.19]; IV: 1.37 + 0.24 + 1.61 + 1.36 + 0.88 = [5.46]; pedipalpus: 0.58 + 0.23 + 0.45 + 0.50 = [1.76]. Femur I 1.83 × carapace width, palpal femur 0.75 × carapace width.

Abdomen 1.31 long, 0.96 wide. Atrium 0.19 long, 0.24 wide, spermathecae 0.17 long (Figs. 106–108).

**Variation ($n$ = 4).**—Total length 2.03–2.53; carapace length 1.0–1.23 × carapace width; OAL 1.0–1.35 × OAW, diameter PME 0.6–0.7 × PLE interdistances; length femur I 1.62–2.08 × carapace width, palpal femur 0.75–0.83 × carapace width; atrium length 0.77–0.79 × width, spermathecae 0.65–0.71 × atrium width.




Figures 89–94.—*Calileptoneta wapiti* (Gertsch), male from Cameron Road, right palpus. 89. retrolateral. 90. ventral. 91. prolateral. 92. retroapical. 93. ventroapical. 94. proapical. AC= apical constriction, AH = apical hook, AL = apical lobe, E = embolus, PF = proapical flange, PL = prolateral lobe, PS = paraembolar setae, RS = retroapical setae. Scale bars: 89–91 = 176 μm, 92–94 = 86 μm.

**Natural history.**—This spider is most commonly found among the dense leaf litter in redwood and Douglas fir forests although they may also be found under moist rotting logs. Individuals in captivity constructed small sheet webs like those of other *Calileptoneta* species. The extremely long palp of the male suggests a mating behavior potentially unique among *Calileptoneta* species.

**Distribution.**—Restricted to redwood (*Sequoia sempervirens*) and mixed evergreen forests (Douglas fir-redwood) on the Pacific northwest coast of California (Fig. 120).

*Calileptoneta oasa* (Gertsch 1974)
Figs. 15, 32–34, 71–76, 102–103, 119

*Leptoneta oasa* Gertsch 1974: 197; Brignoli 1977: 217.

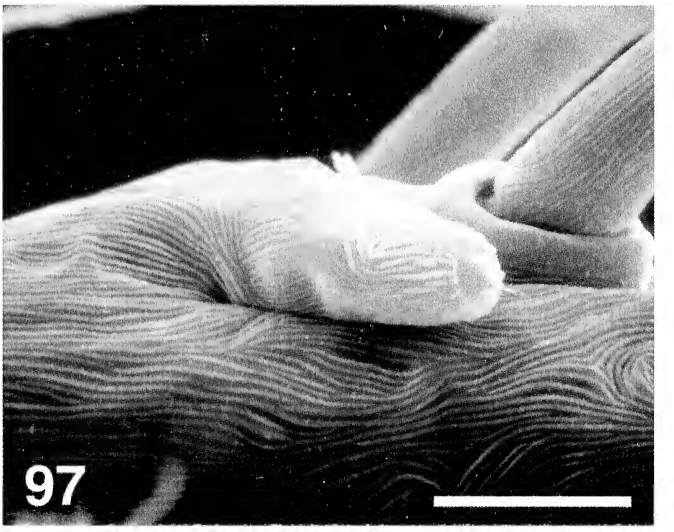
*Calileptoneta oasa* (Gertsch): Platnick 1986: 15; Platnick 2002.

**Type material.**—Male holotype from Andreas Canyon, off Palm Canyon, near Palm Springs, Riverside County, California, USA, 33°49′N, 116°32′W, 26 March 1960, W.J. Gertsch (AMNH, examined). Paratype: USA: *California*: 1 ♀, same data as holotype (AMNH, examined).

**Other material examined.**—USA: *California*: Riverside County: Andreas Canyon, near Palm Springs, 33°49′N, 116°32′W, 3 March 1956, V. Roth (1 ♂, 1 ♀, 1 juvenile, MCZ unique # 35493).

**Diagnosis.**—Distinguished from other *Calileptoneta*, except *C. ubicki*, by having females with a bifid atrium (Fig. 102) and males without a proximal bulb process (Figs. 32–34) or retrolateral twisted tarsal setae on the palpus (Fig. 37); from *C. ubicki* by the following combination of characters: lacking a retrodistal cheliceral apophysis (Fig. 16), having a hook-shaped retroapical tibial seta on the pal-





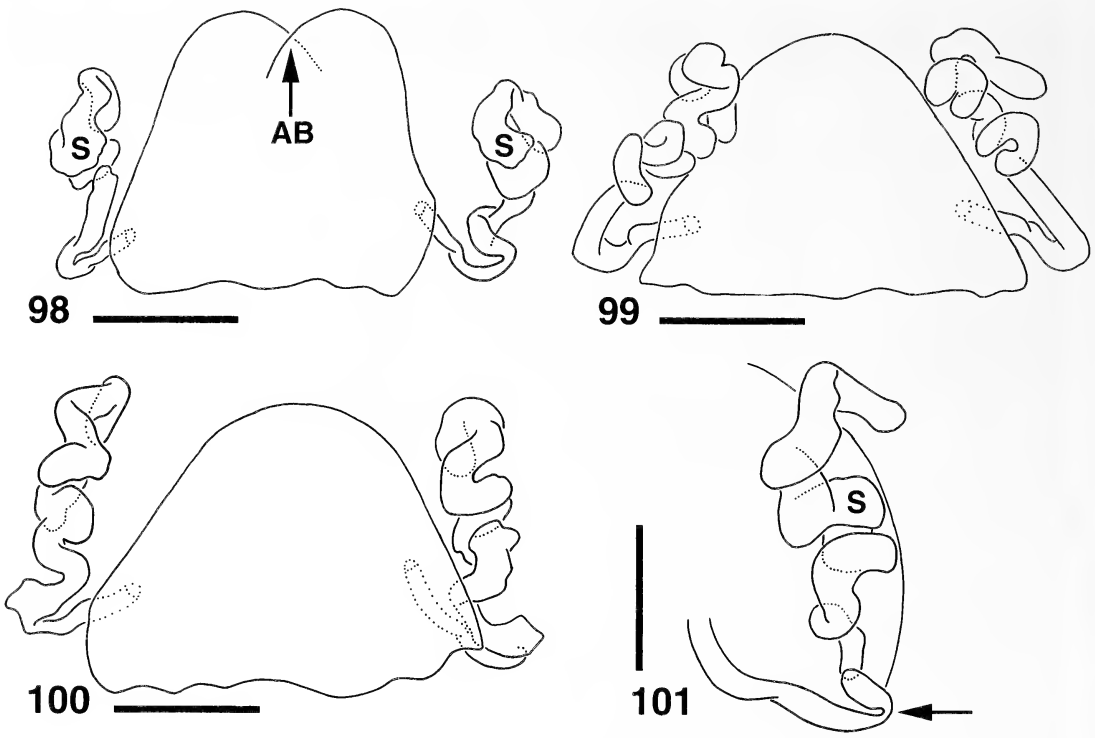

Figures 95–97.—*Calileptoneta* sp., tarsal organs, right palpus, dorsoapical. 95. *C. ubicki* new species, from Arroyo Seco Canyon. 96. *C. noyoana* (Gertsch), from Fort Bragg. 97. *C. sylva* (Chamberlin & Ivie), from Samwell Cave. Scale bars: 95 = 7.5 μm, 96 = 10 μm, 97 = 8.6 μm.

pus (Fig. 71), and having the proapical flange straight anteriorally (Fig. 76).

**Male (holotype).**—Total length 1.70. Specimen faded. Carapace yellow-brown with dusky mottling surrounding margin, and laterally along caput margins; clypeus with dusky mottling distally; sternum dusky; coxae, trochanters, leg segments, and palpi yellow-brown.

Carapace 0.75 long, 0.62 wide, height at fovea 0.54 × carapace width; clypeus 0.12 high, chelicerae 0.45 long, fang furrow with 5 teeth along a narrow ridge and 1 denticles on retromargin (Fig. 15). Ocular area 0.21 long, 0.15 wide; diameter PME 0.75 × PLE interdistances. Sternum 0.48 long, 0.45 wide; labium 0.08 long, 0.15 wide; palpal coxae 0.30 long, 0.15 wide.

Spination: palpus: patella d1; tibia r1-1. Leg measurements (Femur + Patella + Tibia +




Figures 98–101.—*Calileptoneta* sp., female genitalia, ventral. 98. *C. ubicki* new species, from Arroyo Seco Canyon. 99. *C. californica* (Banks), from Bell Station. 100. *C. noyoana* (Gertsch), from Fort Bragg. 101. *C. noyoana* (Gertsch), from Fort Bragg, left lateral, arrow to sharp bend in spermathecae. AB = apical bifurcation, S = spermathecae. Scale bars: 98 = 0.08 mm, 99 = 0.10 mm, 100 = 0.12 mm, 101 = 0.08 mm. Illustrations by JL.

Metatarsus + Tarsus = [Total]): I: 1.83 + 0.24 + 1.85 + 1.65 + 0.98 = [6.55]; II: 1.37 + 0.24 + 1.51 + missing + missing = [N/A]; III: 1.12 + 0.20 + 1.05 + 1.0 + 0.61 = [3.98]; IV: 1.46 + 0.20 + 1.07 + 1.0 + 0.61 = [4.34]; pedipalpus: 0.42 + 0.15 + 0.20 + 0.29 = [1.06]. Femur I 2.95 × carapace width, palpal femur 0.68 × carapace width.

Palpal bulb (Figs. 71–76) 0.36 long, 0.20 wide; palpal tibia with a retroapical hook-shaped seta; embolus tapering to a sharp point (Fig. 75); paraembolar setae fan-like with 3 sagitate setae extending to apex of embolus (Fig. 76); accessory lobe reduced.

Abdomen dusky with pale chevron pattern, 0.95 long, 0.77 wide.

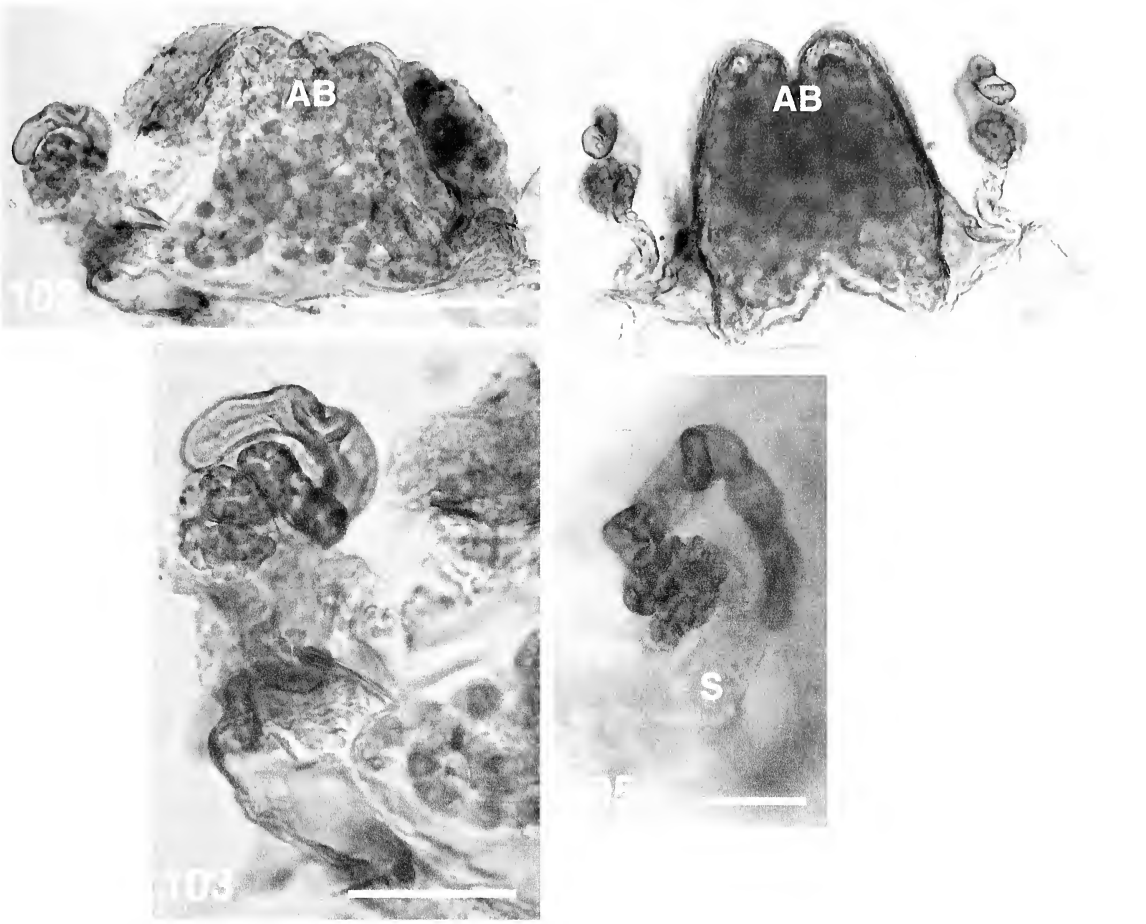
**Variation (*n* = 2).**—Total length 1.70–1.71; carapace length 1.21–1.23 × carapace width; OAL 1.08–1.40 × OAW, diameter PME 0.66–0.77 × PLE interdistances; length femur I 2.79–3.0 × carapace width, palpal femur 0.68–0.69 × carapace width; bulb length 1.80–2.20 × palpal tibia length.

**Female (paratype).**—Total length 1.28. Specimen faded. Coloration and markings same as male.

Carapace 0.69 long, 0.59 wide, height at fovea 0.50 × carapace width; clypeus 0.11 high, chelicerae 0.33 long, fang furrow with 6 teeth on a narrow ridge and 4 denticles on retromargin (Fig. 15). Ocular area 0.18 long, 0.14 wide; diameter PME 0.62 × PLE interdistances. Sternum 0.45 long, 0.42 wide; labium 0.05 long, 0.15 wide; palpal coxae 0.25 long, 0.13 wide.

Spination: palpus: patella d1, tarsus p1, r1-1, v2-1. Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.29 + 0.22 + 1.39 + 1.12 + 0.78 = [4.8]; II: 1.0 + 0.20 + 1.0 + 0.83 + 0.61 = [3.64]; III: 0.89 + 0.20 + 0.78 + 0.71 + 0.51 = [3.09]; IV: 1.17 + 0.20 + 1.02 + 0.90 + 0.49 = [3.78]; pedipalpus: 0.41 + 0.12 + 0.22 + 0.38 = [1.13]. Femur I 2.19 × carapace width, palpal femur 0.69 × carapace width.

Abdomen 1.19 long, 0.95 wide. Atrium




Figures 102–105.—*Calileptoneta* sp., female genitalia, ventral (102, 104) and left lateral (103, 105). 102–103. *C. oasa* (Gertsch), from Andreas Canyon. 104–105. *C. ubicki* new species, from Arroyo Seco Canyon. AB = apical bifurcation, S = spermatheca. Scale bars: 102 = 0.10 mm, 103 = 0.05 mm, 104 = 0.10 mm, 105 = 0.08 mm.

0.18 long, 0.21 wide, spermathecae 0.12 long (Figs. 102–103).

**Variation (*n* = 2).**—Total length 1.28–1.72; carapace length 1.17–1.22 × carapace width; OAL 1.24–1.29 × OAW, diameter PME 0.62–0.70 × PLE interdistances; length femur I 2.19–2.56 × carapace width, palpal femur 0.69–0.72 × carapace width.

**Natural history.**—Unknown.

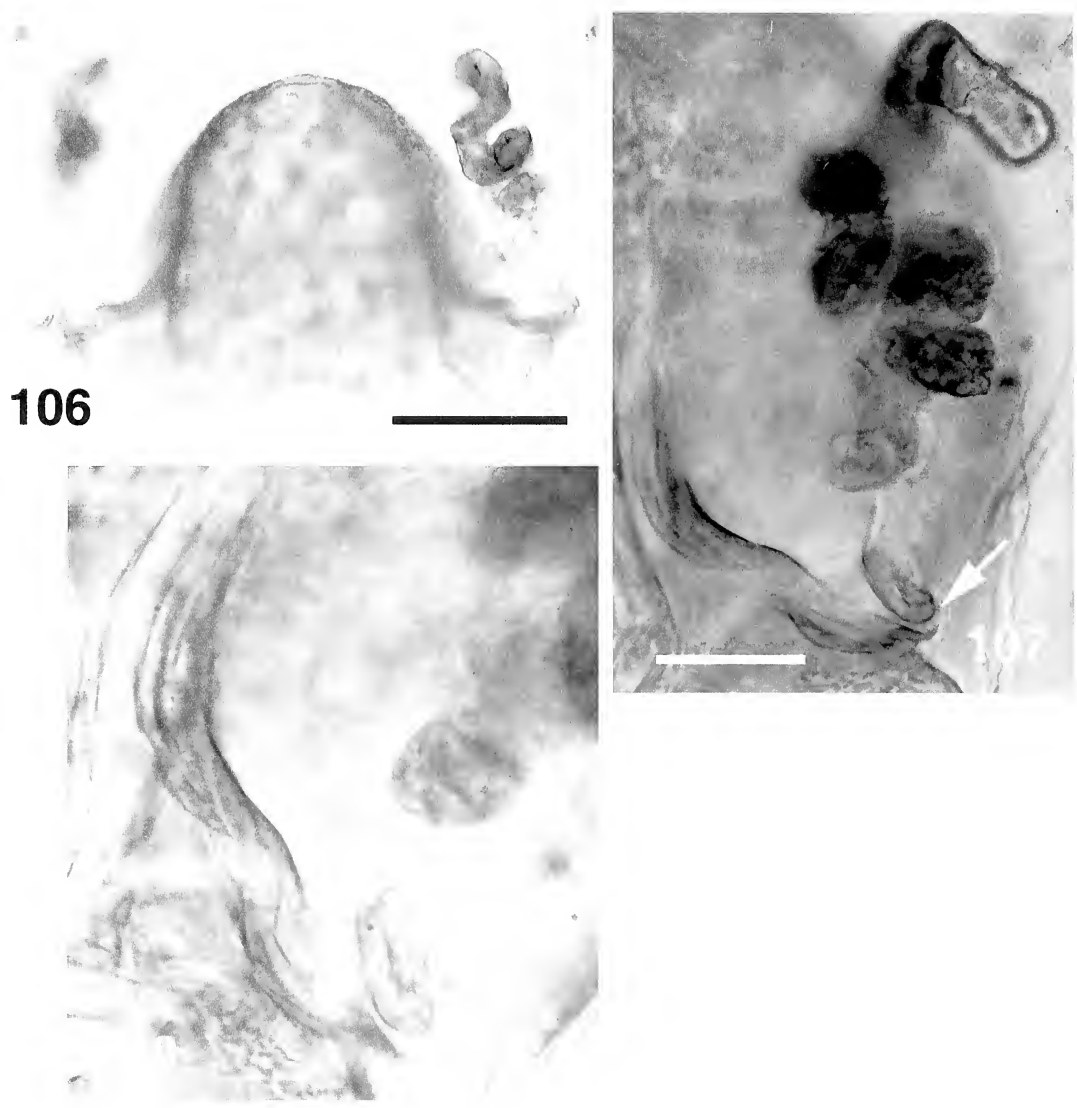
**Distribution.**—Known only from the type locality (Fig. 119).

*Calileptoneta sylva* (Chamberlin & Ivie 1942)
Figs. 23, 77–82, 97, 109–110, 121

*Leptoneta sylva* Chamberlin & Ivie 1942: 9–10.
*Leptoneta californica* (Chamberlin & Ivie): Gertsch 1974: 191 (misidentification, not *L. californica* Banks 1904).
*Calileptoneta californica* (Chamberlin & Ivie) (part): Platnick 1986: 14; Platnick 2002.

**Type material.**—Female holotype, 19 miles N. Wolf Creek, Jackson County, Oregon, USA, 42°42′N, 122°57′W, 6 April 1937, J.C. Chamberlin (holotype female, AMNH).

**Other material examined.**—USA: *California*: Shasta County: Samwell Cave, 40°55′N, 122°14′W, 14 April 2000, J.M. Ledford, at entrance under limestone (1 ♂, 2 juveniles, CASC); *Oregon*: Jackson County: Ashland watershed, T39S, R1E, SEC 34, PFT #46, 20 July 1998, R.W. Peck et al. (1 ♂, OSU); Jenny Creek LSR, Medford district, 41°58′N, 122°24′W, BLM, LS, Oldgrowth, T39S, R03E, SEC 35, PFT 31–40, 21–23 June

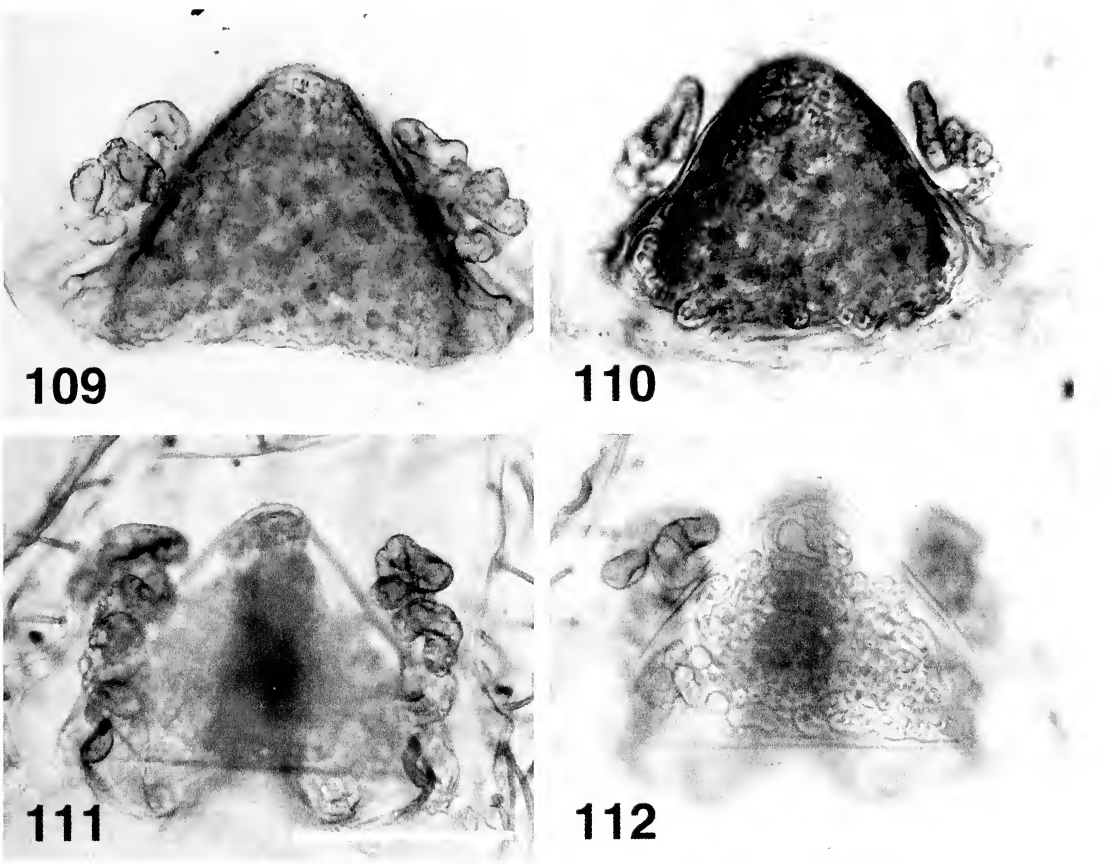



Figures 106–108.—*Calileptoneta noyoana* (Gertsch), female genitalia, ventral (106) and left lateral (107, 108). Arrow in 107 to sharp bend in spermatheca. Scale bars: 106 = 0.10 mm, 107 = 0.05 mm, 108 = 0.025 mm.

1999, B. Peck (1 ♂, OSU); Jenny Creek LSR, Medford district, 41°58′N, 122°24′W, BLM, LS, Oldgrowth, T39S, R03E, SEC 35, traps 21–3–0, 16–18 August 1999, B. Peck (1 ♀, OSU).

**Diagnosis.**—Distinguished from other *Calileptoneta*, except *C. briggsi*, *C. californica*, and *C. helferi*, by males having a proximal bulb process (Figs. 38–40, 77–79) and a straight retroapical seta (Figs. 39, 78); from *C. californica* and *C. helferi* by having the proximal bulb process (Figs. 77–79) short, process length 0.55–0.86 × bulb width, and having the prolateral apical lobe large (Figs. 46, 82); from *C. briggsi* by being darkly pigmented and having a straight, distally narrowed embolus with a slight prolateral bend (Fig. 81).

**Male (Samwell Cave).**—Total length 2.17. Carapace yellow-brown with fine dusky mottling surrounding margin, and laterally along caput margins; clypeus with dusky mottling distally; sternum dusky; coxae, trochanters, legs, and pedipalpi with dusky mottling, being especially conspicuous at the bases and apices of the segments.




Figures 109–112.—*Calileptoneta* sp., female genitalia, ventral. 109. *C. sylva* (Chamberlin & Ivie) holotype. 110. *C. sylva* (Chamberlin & Ivie), from Jenny Creek. 111–112. *C. briggsi* new species from Indian Valley Creek Cave. Scale bars: 109–110 = 0.10 mm, 111–112 = 0.12 mm.

Carapace 1.0 long, 0.90 wide, height at fovea 0.24 × carapace width; clypeus 0.14 high, chelicerae 0.57 long, fang furrow with 9 teeth along a narrow ridge and 4 denticles on retromargin (Fig. 23). Ocular area 0.26 long, 0.22 wide; diameter PME 0.64 × PLE interdistances. Sternum 0.65 long, 0.62 wide; labium 0.10 long, 0.19 wide; palpal coxae 0.47 long, 0.21 wide.

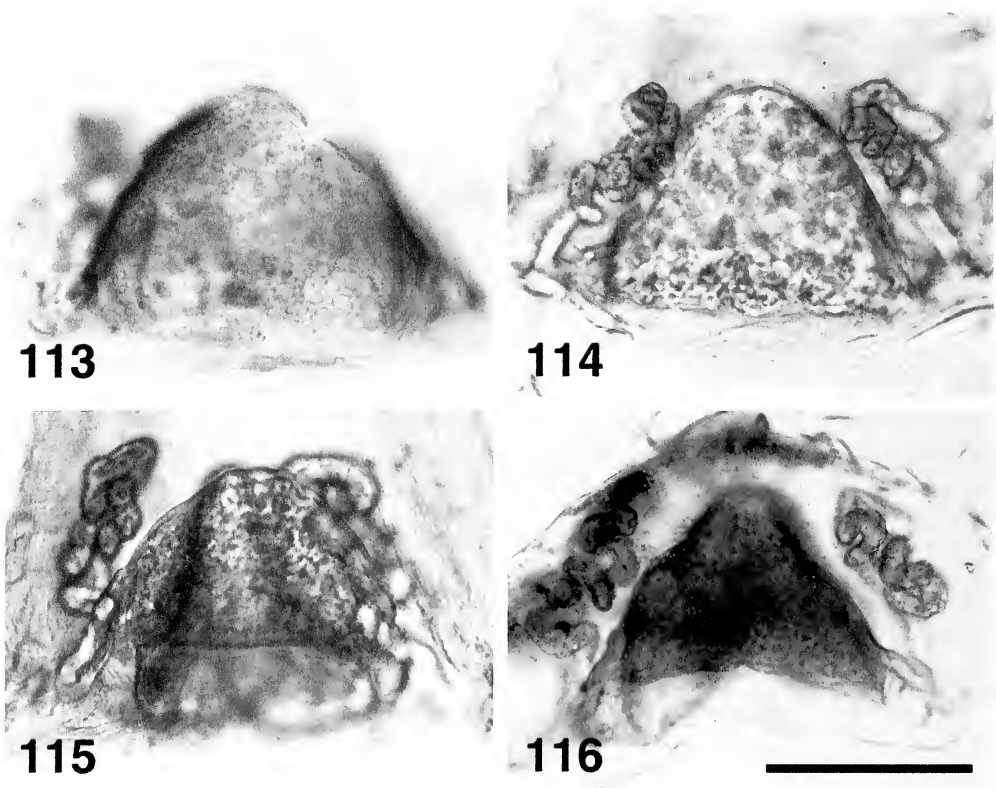
Spination: palpus: femur p1-3-2-1-2-1-2-2-2, r5-3-2-2 (apical), v1 (apical); patella d1; tibia r1-2-1-1-3; tarsus r1 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 2.36 + 0.34 + 2.72 + 2.18 + 1.15 = [8.75]; II: 1.74 + 0.32 + 1.74 + 1.47 + 0.88 = [6.15]; III: 1.43 + 0.28 + 1.29 + 1.21 + 0.73 = [4.94]; IV: 1.81 + 0.30 + 1.77 + 1.61 + 0.95 = [6.44]; pedipalpus: 0.95 + 0.36 + 0.49 + 0.63 = [2.43]. Femur I 2.62 × carapace width, palpal femur 0.1.05 × carapace width.

Palpal bulb (Figs. 77–82) 0.61 long, 0.22 wide; palpal tibia with a retroapical group of stiff setae; proximal bulb process short, reaching to base of tibia, bulb length 1.24 × length tibia; embolus distally narrowed with a slight prolateral bend; paraembolar setae circular, distally broad, reaching to apex of embolus (Fig. 82).

Abdomen dusky with pale chevron pattern, 1.17 long, 0.89 wide.

**Variation (*n* = 2).**—Total length 2.04–2.17; OAL 1.18–1.23 × OAW, diameter PME 0.50–0.64 × PLE interdistances; length femur I 2.16–2.72 × carapace width, palpal femur 0.96–1.05 × carapace width; palpal bulb length 1.20–1.24 × palpal tibia length; proximal bulb process length 0.55–0.86 × bulb width.

**Female (holotype).**—Total length 2.69. Specimen faded. Carapace yellow-brown with dusky mottling surrounding margin, and lat-




Figures 113–116.—*Calileptoneta* sp., female genitalia, ventral. 113. *C. californica* (Banks) from Oakville. 114. *C. californica* (Banks) from Bell Station. 115. *C. helferi* (Gertsch) from Fault Rock Cave. 116. *C. helferi* (Gertsch) from Claremont Avenue. Scale bar = 0.10 mm.

erally along caput margins; clypeus with dusky mottling distally; sternum yellow-brown; coxae, trochanters, leg segments, and palpi yellow-brown.

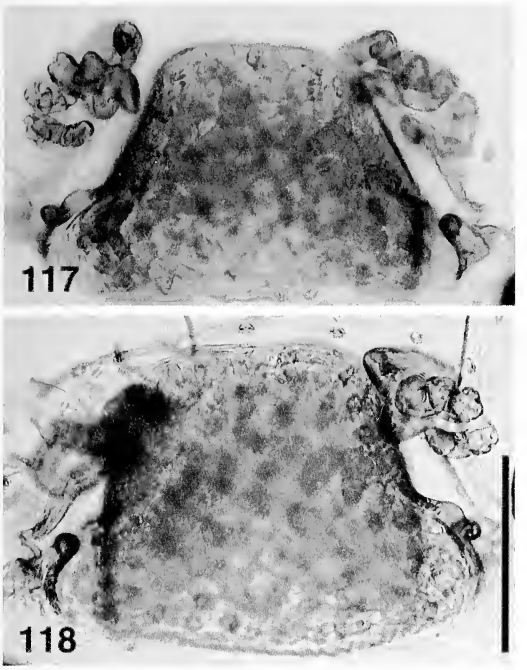
Carapace 1.05 long, 0.92 wide, height at fovea 0.26 × carapace width; clypeus 0.10 high, chelicerae 0.61 long, fang furrow with 9 teeth on a narrow ridge and 2 denticles on retromargin (Fig. 23). Ocular area 0.28 long, 0.23 wide; diameter PME 0.54 × PLE interdistances. Sternum 0.65 long, 0.59 wide; labium 0.10 long, 0.16 wide; palpal coxae 0.45 long, 0.23 wide.

Spination: palpus: patella d1, tarsus p2-1-1, r1-1, v1-2 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.77 + 0.34 + 2.0 + 1.61 + 1.07 = [6.79]; II: 1.41 + 0.34 + missing + missing + missing = [N/A]; III: 1.29 + 0.28 + 1.21 + 1.11 + 0.75 = [4.64]; IV: 1.70 + 0.32 + 1.70 + 1.47 + 0.91 = [6.10]; pedipalpus: 0.66 + 0.23 + 0.47 + 0.59 = [1.95]. Femur I 1.92 × carapace width, palpal femur 0.72 × carapace width.

Abdomen 1.64 long, 1.53 wide. Atrium 0.19 long, 0.20 wide, spermathecae 0.16 long (Fig. 109).

**Variation (*n* = 2).**—The only known female besides the holotype (Jenny Creek) is badly damaged and missing most appendages. Atrium 0.19 long, 0.20 wide, spermathecae 0.14 long (Fig. 110).

**Remarks.**—Gertsch (1974) synonymized *L. sylva* with *L. californica* based on the similarity in abdominal pattern and female genitalia between the type of *L. sylva* and a topotypic female of *L. californica* (Mt. Diablo). The type of *L. californica* was lost at the California Academy of Sciences during the 1906 earthquake and fire. Since the abdominal patterns within *Calileptoneta* species are variable, and the female genitalia for species outside the *oasa* group do not allow specific diagnosis, I consider the synonymy of these




Figures 117–118.—*Calileptoneta cokendolpheri* new species, female genitalia, ventral. 117–118. Females from H. J. Andrews, showing intraspecific variation. Scale bar = 0.12 mm.

species unjustified. Additionally, males belonging to the californica group, clearly different from the species treated in this paper, have been recently discovered near the type locality of *L. sylva*. Instead of assigning a new name to this species, they are placed with *L. sylva*.

**Natural history.**—The male from Samwell Cave, Shasta County was collected under limestone at the cave entrance that remains cool and moist throughout the year. No specimens have ever been taken inside the cave despite extensive arachnid surveys.

**Distribution.**—Southern Oregon to north-central California (Fig. 121).

***Calileptoneta ubicki*** new species
Figs. 1, 2, 3, 16, 83–88, 95, 98, 104, 105, 119

**Type material.**—Male holotype from Arroyo Seco Canyon Campground, SW of Lakes, Monterey County, California, USA, 36°14′N, 121°28′W, 22 January 2001, J.M. Ledford, P. Marek (CASC).

**Other material examined.**—USA: *California*: Monterey County: Arroyo Seco Campground, SW of Lakes, 36°14′N, 121°28′W, 900 ft. elevation, under granite, 6 May 1995, D. Ubick, W. Savary (1 ♂, DU), 22 January 2001, J.M. Ledford, P. Marek (2 ♀, CASC).

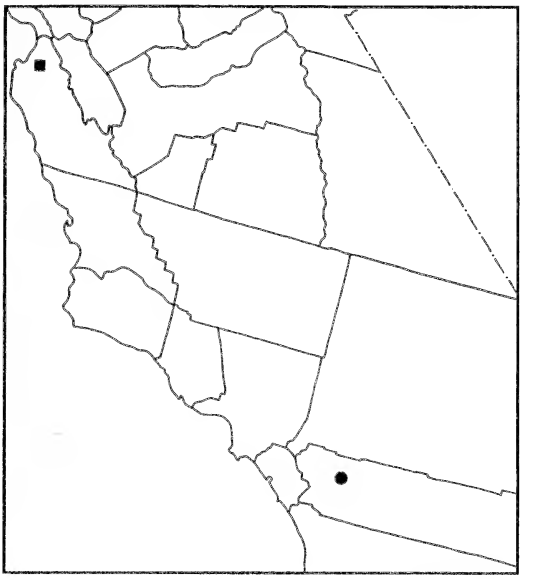


Figure 119.—Distribution map for *Calileptoneta oasa* (Gertsch), and *Calileptoneta ubicki* new species ● = *C. oasa*, ■ = *C. ubicki*.

**Etymology.**—This species is named in honor of Mr. Darrell Ubick, collector of this and many other leptonetid spiders throughout California.

**Diagnosis.**—Distinguished from other *Calileptoneta*, except *C. oasa*, by having females with a bifid atrium (Figs. 98, 104), and males without a proximal bulb process (Figs. 32–34, 83–88) or retrolateral twisted tarsal setae on the palpus (Fig. 37); from *C. oasa* by males having a retrodistal cheliceral apophysis (Fig. 16), a whip-shaped retroapical tibial seta on the palpus (Fig. 86), and having a sinuate proapical flange (Fig. 88).

**Male (holotype).**—Total length 2.31. Carapace yellow-brown with a fine dusky band surrounding margin, and laterally along caput margins; clypeus with faint dusky mottling distally; sternum dusky; coxae, trochanters, legs, and pedipalpi with dusky mottling, being especially conspicuous at the bases and apices of the segments.

Carapace 1.08 long, 0.91 wide, height at fovea 0.44 × carapace width; clypeus 0.19 high, chelicerae 0.93 long, fang furrow with 7 teeth along a narrow ridge and 5 denticles and a large distal tooth on retromargin (Fig. 16). Oc-

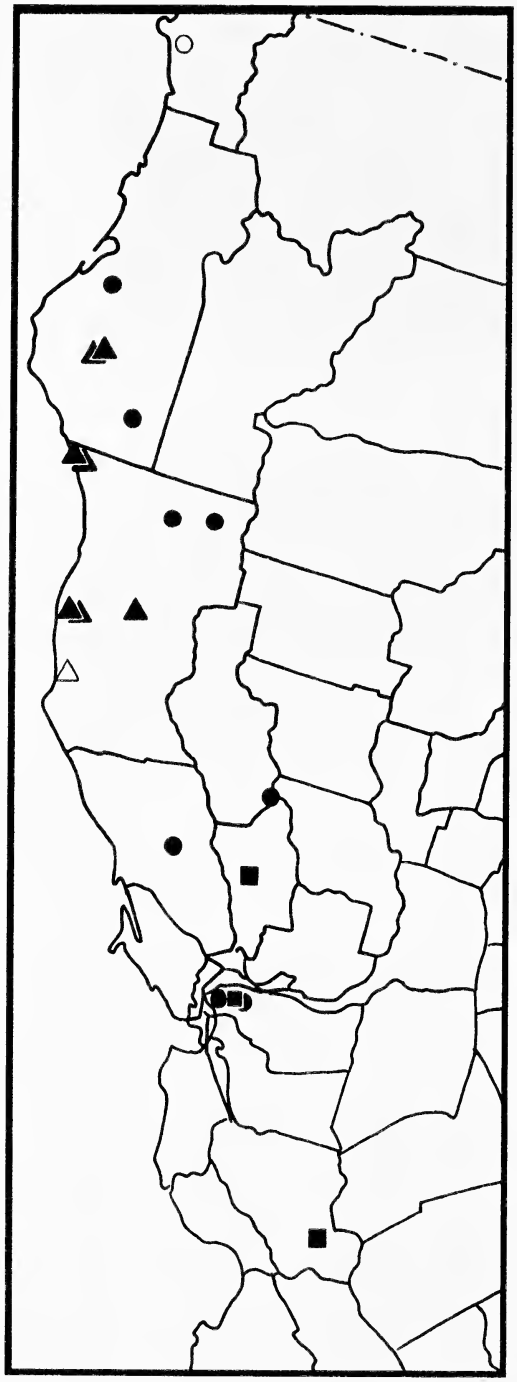


Figure 120.—Distribution map for *Calileptoneta* sp. ■ = *C. californica* (Banks), ● = *C. helferi* (Gertsch), ○ = *C. californica incertae sedis*, ▲ = *C. noyoana* (Gertsch), Δ = *C. wapiti* (Gertsch).

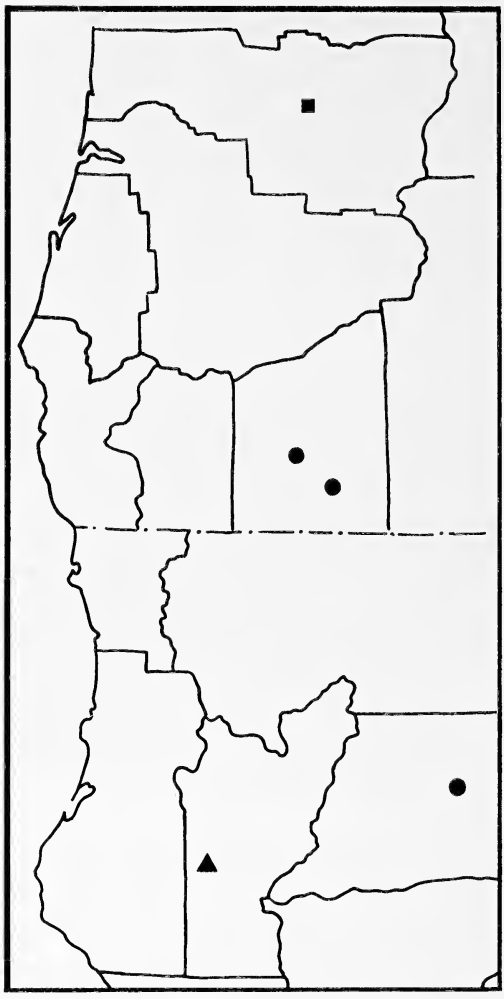


Figure 121.—Distribution map for *Calileptoneta briggsi* new species, *Calileptoneta cokendolpheri* new species, and *Calileptoneta sylva* (Chamberlin & Ivie). ▲ = *Calileptoneta briggsi*, ■ = *C. cokendolpheri*, ● = *C. sylva*.

ular area 0.23 long, 0.22 wide; diameter PME 0.53 × PLE interdistances (Fig. 2). Sternum 0.67 long, 0.63 wide; labium 0.12 long, 0.19 wide; palpal coxae 0.53 long, 0.17 wide.

Spination: palpus: patella d1, tibia r1-1-1. Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 2.41 + 0.34 + 2.80 + 2.43 + 1.29 = [9.27]; II: 1.80 + 0.29 + 1.95 + 1.70 + 0.98 = [6.72]; III: 1.54 + 0.24 + 1.44 + 1.41 + 0.85 = [5.48]; IV: 2.0 + 0.32 + 1.90 + 1.80 + 1.0 = [7.02]; pedipalpus: 0.71 + 0.21 + 0.38 + 0.36 = [1.66]. Femur I 1.09 × carapace width, palpal femur 0.78 × carapace width.

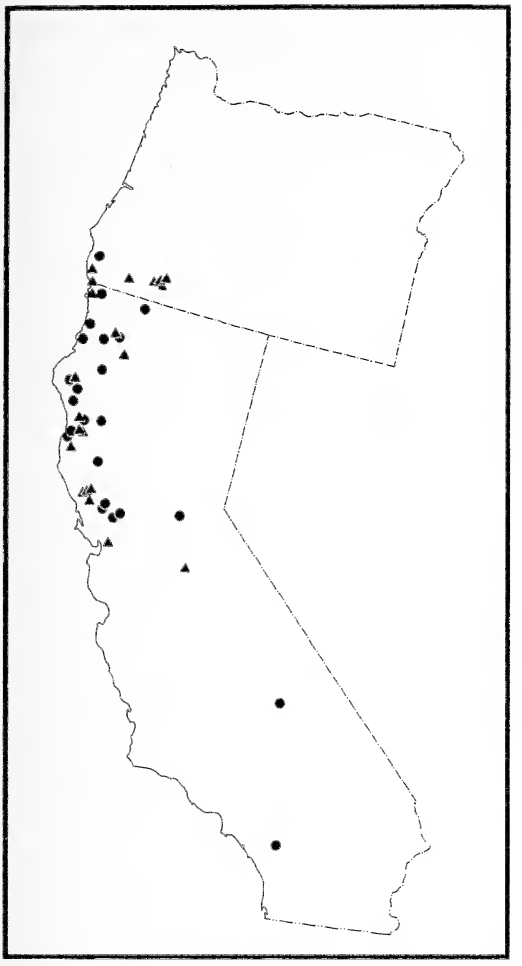


Figure 122.—Distribution map for undiagnosable females and juvenile Calileptoneta sp. ▲= undiagnosable females, ● = juveniles.

Palpal bulb (Figs. 83–88) 0.42 long, 0.25 wide; palpal tibia with a retroapical whip-shaped seta; embolus tapering to a sharp point; paraembolar setae fan-like with 3 clavate setae (Fig. 88); proapical flange sinuate (Fig. 88); accessory lobe reduced.

Abdomen pale with a dusky chevron pattern (Fig. 2), 1.23 long, 1.07 wide.

**Variation (*n* = 2).**—Total length 2.30–2.31; carapace length 1.17–1.19 × carapace width; OAL 1.04–1.05 × OAW, diameter PME 0.50–0.53 × PLE interdistances; length femur I 2.65–2.67 × carapace width, palpal femur 0.75–0.78 × carapace width; bulb length 1.30–1.56 × palpal tibia length.

**Female (paratype).**—Total length 2.31. Coloration and markings same as male.

Carapace 0.80 long, 0.68 wide, height at fovea 0.41 × carapace width; clypeus 0.12 high, chelicerae 0.31 long, fang furrow with 8 teeth along retromargin and 4 denticles (Fig. 16). Ocular area 0.18 long, 0.19 wide; diameter PME 0.50 × PLE interdistances. Sternum 0.50 long, 0.47 wide; labium 0.06 long, 0.14 wide; palpal coxae 0.28 long, 0.13 wide.

Spination: palpus: patella d1, tarsus p1-1-1, r1-1-1-v2 (apical). Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.60 + 0.27 + 1.70 + 1.46 + 0.98 = [6.01]; II: 1.24 + 0.22 + 1.21 + 1.07 + 0.78 = [4.52]; III: 1.07 + 0.22 + 0.93 + 0.90 + 0.83 = [3.95]; IV: 1.4 + 0.22 + 1.24 + 1.15 + 0.80 = [4.81]; pedipalpus: 0.42 + 0.14 + 0.29 + 0.50 = [1.35]. Femur I 2.4 × carapace width, palpal femur 0.62 × carapace width.

Abdomen 1.51 long, 1.13 wide. Atrium 0.19 long, 0.17 wide, spermathecae 0.14 long (Fig. 104).

**Variation (*n* = 2).**—Total length 2.31–2.40; carapace length 1.22–1.18 × carapace width; OAL 0.95–1.0 × OAW, diameter PME 0.50 × PLE interdistances; length femur I 2.24–2.47 × carapace width, palpal femur 0.62–0.71 × carapace width; atrium length 1.0–1.12 × width, spermathecae 0.75–0.82 × atrium width.

**Natural history.**—These spiders were found under moist rocks on a loose granitic slope. Individuals hung beneath tightly woven sheet webs 3–4cm in diameter (Fig. 1).

**Distribution.**—Known only from the type locality (Fig. 119).

*Calileptoneta wapiti* (Gertsch 1974)
Figs. 18, 35–37, 89–94, 120

*Leptoneta wapiti* Gertsch 1974: 195; Brignoli 1977: 217.

*Calileptoneta wapiti* (Gertsch): Platnick 1986: 15; Platnick 2002.

**Type material.**—Male holotype from Cameron Road, near Elk, Mendocino County, California, USA, 39°07′N, 123°43′W, 16 February 1967, V. Roth (AMNH, examined).

**Other material examined.**—USA: *California*: Mendocino County: Mendocino, 39°18′N, 123°47′W, 4 January 1958, J. P. Helfer (1 ♂, AMNH).

**Diagnosis.**—Distinguished from other *Calileptoneta*, except *C. noyoana*, by having males with retrolateral twisted tarsal setae on

the palpus (Figs. 37, 92) and an enlarged distal cheliceral tooth (Fig. 18); from *C. noyoana* by having a short palpal femur, 0.63–1.0 × carapace width.

**Male (holotype).**—Total length 1.91. Specimen faded. Carapace and all appendages yellow-brown.

Carapace 1.31 long, 0.79 wide, height at fovea 0.38 × carapace width; clypeus 0.19 high, chelicerae 0.63 long, fang furrow with 7 teeth on a narrow ridge and 3 denticles on retromargin (Fig. 18). Ocular area 0.22 long, 0.18 wide; diameter PME 0.05 × PLE interdistances. Sternum 0.59 long, 0.57 wide; labium 0.10 long, 0.15 wide; palpal coxae 0.46 long, 0.19 wide.

Spination: palpus: patella d1; tibia r1-1. Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 1.78 + 0.29 + 1.90 + 1.49 + 0.98 = [6.44]; II: 1.80 + 0.29 + 1.44 + 1.20 + 0.80 = [5.53]; III: 1.15 + 0.27 + 1.07 + 1.02 + 0.73 = [4.24]; IV: 1.49 + 0.24 + 1.46 + 1.29 + 0.85 = [5.33]; pedipalpus: 0.78 + 0.29 + 0.42 + 0.36 = [1.85]. Femur I 2.25 × carapace width, palpal femur 1.0 × carapace width.

Palpal bulb (Figs. 89–94) 0.45 long, 0.27 wide; retroapical seta proximally broad and tapering to a point distally; embolus broadly forked at apex; paraembolar setae circular, reaching to base of fork on embolus; accessory lobe small (Fig. 94).

Abdomen dark, without chevron pattern, 1.16 long, 0.91 wide.

**Variation ($n$ = 2).**—Total length 1.91; carapace length 1.20–1.66 × carapace width; OAL 1.22–1.36 × OAW, diameter PME 0.50–0.75 × PLE interdistances; length femur I 2.09–2.25 × carapace width, palpal femur 0.67–1.0 × carapace width, bulb length 1.0–1.07 × palpal tibia length.

**Female.**—Unknown.

**Natural history.**—Trips to relocate this rare species have proven unsuccessful. Specimens originally determined as *C. wapiti* by Gertsch (1974) were females and juveniles with no diagnostic features. Furthermore, these specimens fit into the geographical range of *C. helferi* and *C. noyoana* (Fig. 120). Due to the difficulty in the determination of females and the sympatric distribution of these species in Mendocino County, no female specimens are currently assigned to *C. wapiti*.

**Distribution.**—Mendocino County, Northern California (Fig. 120).

## ACKNOWLEDGMENTS

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Additional fieldwork was a central component of this study and I wish to thank Mr. Paul Marek (CAS), Dr. Tom Briggs (CAS), Mr. Joel Despain (NPS), Ms. Karin Ledford, and especially Mr. Darrell Ubick (CAS) and Ms. Suzanne Ubick (CAS) for assistance in the field. All habitus illustrations are by Ms. Virginia Kirsch. Mr. Darrell Ubick (CAS) assisted with the scanning electron microscope. Mr. James Cokendolpher, Mr. Darrell Ubick (CAS) and Dr. Norman Platnick (AMNH) provided suggestions and helped interpret the oftentimes difficult morphology of these spiders. Dr. Charles Griswold (CAS), Dr. Greg Spicer (SFSU) and Dr. Bob Patterson (SFSU), served as advisors on my thesis committee and assisted in ways too numerous to mention. Finally, I would like to thank Dr. Charles Griswold, Ms. Karin Ledford, Mr. Darrell Ubick, Ms. Suzanne Ubick and the students and staff at the California Academy of Sciences for encouragement and, without whom, this study would not have been possible.

I would like to dedicate this study to the memory of Dr. Willis Gertsch, discoverer of many remarkable spider taxa throughout North America, and an inspiration to generations of American arachnologists.

A draft of this manuscript was critically read by James Cokendolpher, Charles Griswold, Bob Patterson, Greg Spicer and Darrell Ubick.

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# THREE NEW SPECIES OF THE SPIDER GENUS *PHRUROLITHUS* FROM CHINA (ARANEAE, CORINNIDAE)

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**ABSTRACT.** Three new species of the genus *Phrurolithus* are described from the Gaoligong Mountain Region of Yunnan Province, China: *Phrurolithus bifidus*, *P. qiqiensis* and *P. revolutus*.

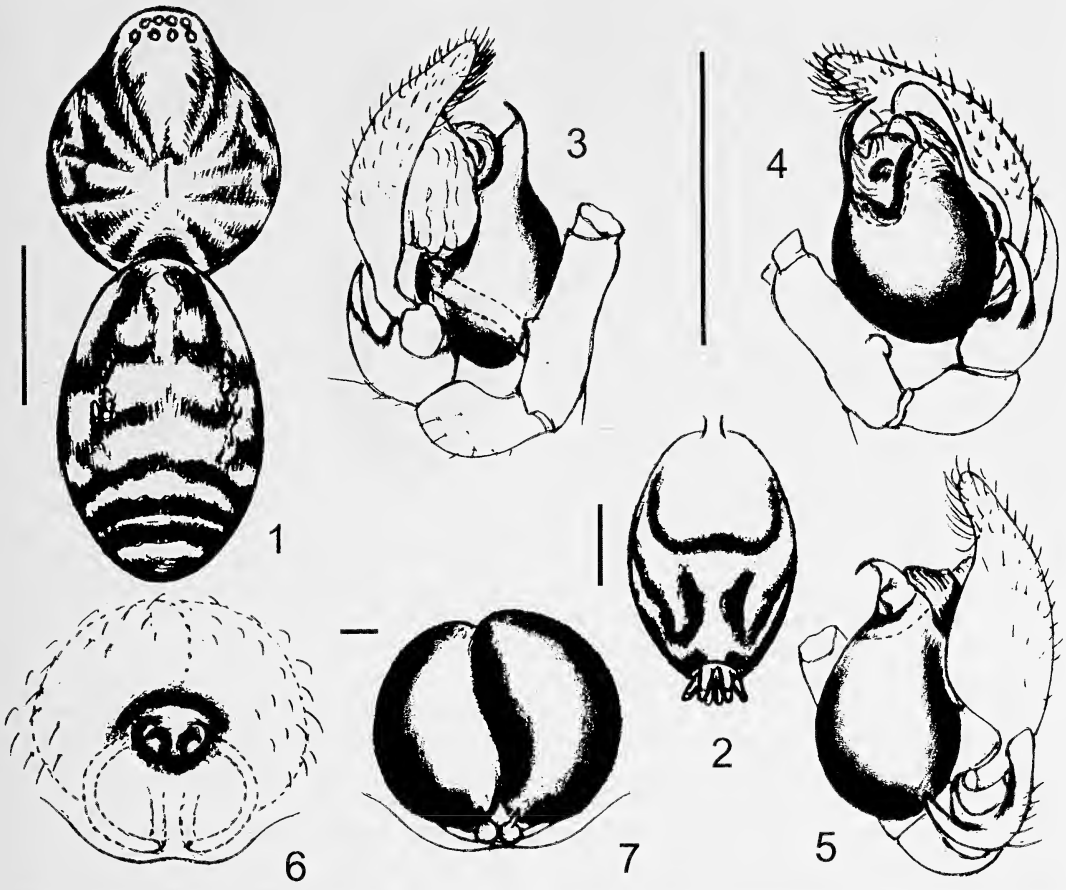
**Keywords:** Taxonomy, Asia, Yunnan, Gaoligong Mountains

The genus *Phrurolithus* C.L. Koch 1839, with some 70 described species, is currently the largest phrurolithine genus in the northern hemisphere (Platnick 2002). This richness, however, is deceptive as most of the species are probably not closely related to the type species, *P. festivus* (C.L. Koch 1835). For instance, the New World species currently in *Phrurolithus*, and representing over half of the taxa, are most probably all misplaced; some have already been formally reassigned to *Scotinella* Banks (Dondale & Redner 1982) and the others will no doubt follow. Additionally, some of the European species have recently been removed to *Liophrurillus* Wunderlich 1992 and *Phrurolinillus* Wunderlich 1995 (Wunderlich 1992, 1995) and some Asian ones to *Otacilia* Thorell 1897 (Deeleman-Reinhold 2001) and what remains is probably still far from being monophyletic. For example, the 14 species currently recorded from China exhibit a wide spectrum of genitalic forms (Song, Zhu & Chen 1999). Males range in having the palpal tibial apophysis represented by a single large process, similar to that in *P. festivus* (see figs. 240I–J in Song, Zhu & Chen 1999), to being polyfurcate (*P. liaoningensis* Song, Zhu & Chen 1999; see figs. 240M–N, in Song, Zhu & Chen 1999), to having one strongly reduced process (*P. splendidus* Song & Zheng 1992; see figs. 241C–D, in Song, Zhu & Chen 1999), to completely lacking a process (*P. daoxianensis* Yin, Peng, Gong & Kim. 1997; see figs. 240G–H, Song, Zhu & Chen 1999). Similarly, and as would be expected, the female genitalia are equally diverse, with extreme variation in spermathecal size, the form of accessory bursae, and length and coiling of copulatory ducts. Given this morphological diversity, it is with some hesitation that we are placing the three new species in *Phrurolithus*. Whereas the three species do all have a pair of large spermathecae, as in *P. festivus*, the tibial apophysis of *P. bifidus*, the only male here described, is bifurcate and deviates significantly from that of the type species. Although this degree of intrageneric genitalic variation was accepted for *Otacilia* by Deeleman-Reinhold (2001), it remains to be seen if future studies will reveal a similar trend in *Phrurolithus*.

The new species here described were collected in the Gaoligong Mountains by the first and second Sino-American expeditions. The type specimens are deposited in the College of Life Science at the Hunan Normal University and some paratypes at the California Academy of Sciences. This is Scientific Contribution no. 27 from the California Academy of Sciences Center for Biodiversity Research and Information and contribution no. 20 from the China Natural History Project.

## METHODS

Specimens were killed in 75% ethanol and after 24 hours transferred to 85% ethanol for




Figures 1–7.—*Phrurolithus bifidus*, new species. 1–5. Male. 1. Body, dorsal view. 2. Abdomen, ventral view. 3–5. Palpus. 3. Prolateral view. 4. Retrolateral, subventral view. 5. Retrolateral, subdorsal view. 6–7. Female. 6. Epigynum. 7. Vulva. Scale lines: 1–5 = 1.00mm; 6, 7 = 0.10mm.

preservation. Epigyna were cleared in lactic acid for examination and stored in microvials with the specimen. Examination was with an Olympus Tokyo BH-2 stereo dissecting microscope. Leg and palpus lengths are given as: total length (femur, patella + tibia, metatarsus, tarsus). All measurements are in mm.

Abbreviations: AER = anterior eye row; AL = abdomen length, ALE = anterior lateral eye, AME = anterior median eye, AME—ALE = distance between AME and ALE, AME—AME = distance between AMEs, AW = abdomen width, CH = clypeus height, CL = carapace length, CW = carapace width, MOQ = median ocular quadrangle, MOQA = MOQ anterior width, MOQL = length of MOQ, MOQP = MOQ posterior width, PER = posterior eye row, PLE = posterior lateral eye, PME = posterior median eye, PME—PLE = distance between PME and PLE, PME—PME = distance between PMEs, RTA = retrolateral tibial apophysis, TL = total length.

### *Phrurolithus bifidus* new species
Figs. 1–7

**Type material.**—Male holotype from sifted leaf litter in native forest on pass over Gaoligongshan, Nankang, 36 air km SE Teng-Chong (24°50′N, 98°47′E, 2100m), Baoshan Prefecture, Yunnan Province, China, 4–7 November 1998, C. Griswold and D. Kavanaugh (deposited in Hunan Normal University, type number 98-NK-48). *Paratypes*: China: *Yunnan Province*: 1 male and 1 female collected with the holotype (female deposited at the Hunan Normal University, male at the California Academy of Sciences).

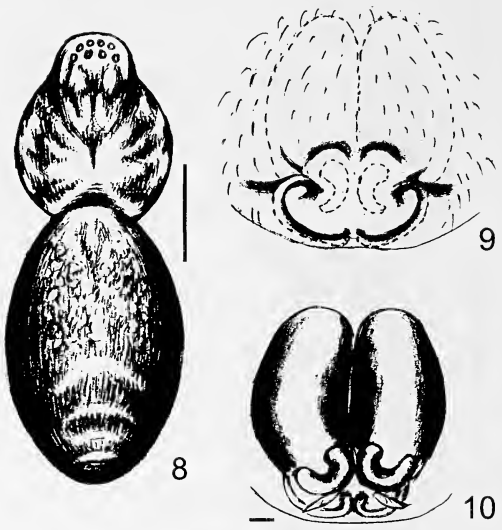
**Etymology.**—The specific name refers to the bifid tibial apophysis of the male palpus.

**Diagnosis.**—The male of this species differs from most other east Asian *Phrurolithus*, except *P. vulpes* Kamura 2001 and *P. pennatus* Yaginuma 1967, in having a bifid tibial apophysis on the palpus. From *P. vulpes* (see Kamura 2001, figs. 1–5) and *P. pennatus* (see Paik 1991, figs. 51–54 and Danilov 1999, fig. 3E–F) it differs in having the retrolateral prong of the RTA almost as long as the dorsal prong (as opposed to less than one third the length of the dorsal prong in the other species), and the dorsal prong apically spatulate (with subapical notch in *P. vulpes* and apically attenuated in *P. pennatus*). The female differs from most Asian *Phrurolithus* in having very large spermathecae and appears most similar to *P. hamdeokensis* Seo 1988 (see Paik 1991, figs. 29–38) as both species have an epigynum with a single central atrium bearing the copulatory openings and spermathecae which are asymmetrical. It differs from *P. hamdeokensis* in having a larger epigynal atrium and larger spermathecae that overlap along their anterior margins.

**Description.**—Male: Carapace pear-shaped, brown with pale gray pattern. AER and PER straight in dorsal view. Cervical groove distinct, head region slightly elevated. Fovea short, longitudinal, anteriorly with bilobed pale mark, laterally with radiating markings along radial grooves. Sternum yellow brown, margins darker with gray radial striae inwards. Chelicera weak, grayish brown, with 1 retromarginal and 3 promarginal teeth. Endites and labium grayish brown. Palpus and leg segments yellow-brown, distal end of leg femur having grayish black annulus, tibia and metatarsus with one dark stria. Anterior leg spines: 4 on prolateral surface of femur, 7 pairs ventrally on tibiae, and 4 pairs ventrally on metatarsi. Abdomen with dorsum grayish black patterned with yellowish gray, anteriorly with pale cardiac mark and lateral spots, posteriorly with five chevrons (Fig. 1); venter yellow gray with dark markings (Fig. 2).

Palpus with large, spherical genital bulb bearing short, curved embolus apically; tibial apophysis large, deeply bifid, with spatulate dorsal and pointed retrolateral prong; femur with small ventral knob about 2/3 the distance from its basal margin (Figs. 3–5).

Female: Coloration and markings as in male, except carapace reddish brown; eye arrangement as male. Epigynum with small sub-




Figures 8–10.—*Phrurolithus qiqiensis*, new species, female. 8. Body, dorsal view. 9. Epigynum. 10. Vulva. Scale line: 8 = 1.00mm; 9, 10 = 0.10mm.

circular atrium (Fig. 6); vulva with two large spermathecae from which thin copulatory ducts extend along semicircular arc to atrium.(Figs. 6–7)

Measurements: Male (holotype): TL 3.90, CL 1.70, CW 1.50; AL 2.10, AW 1.30. Eye sizes and interdistances: AME 0.10, ALE 0.10, PME 0.09, PLE 0.13, AME-AME 0.05, AME-ALE 0.025, PME-PME 0.40, PME-PLE 0.03; MOQL 0.25, MOQA 0.24, MOQP 0.27; CH 0.14, longer than AME diameter. Appendage lengths: palpus: 2.10 (0.50, 0.60, 0, 1.00); leg I: 5.94 (1.68, 2.50, 1.06, 0.70); leg II: 5.50 (1.50, 2.00, 1.30, 0.70); leg III: 4.30 (1.40, 1.50, 0.90, 0.50); leg IV: 6.62 (1.92, 2.00, 1.80, 0.90); leg formula: IV, I, II, III.

Female: TL 4.10, CL 1.60, CW 1.40; AL 2.40, AW 1.40. Appendage lengths: palpus: 1.42 (0.32, 0.60, 0, 0.50); leg I: 4.96 (1.40, 1.71, 1.25, 0.60); leg II: 4.85 (1.35, 1.80, 1.00, 0.70); leg III: 3.70 (1.10, 1.10, 1.00, 0.50); leg IV: 6.10 (1.65, 1.90, 1.70, 0.85); leg formula: IV, I, II, III.

**Distribution.**—Yunnan Province, China.

***Phrurolithus qiqiensis*** new species
Figs. 8–10

**Type material.**—Female holotype collected in Qiqi He, 9.9 air km W of Gongshan (27°43′ N, 98°34′ E, 2000m), Mt. Gaoligong, Nujiang State Nature Reserve, Nujiang Pre-

fecture, Yunnan Province, China, 9–14 July 2000, H.M. Yan, D. Kavanaugh, C.E. Griswold, H.-B. Liang, D. Ubick, and D.-Z. Dong (deposited in Hunan Normal University, type number 00-QF-44). *Paratypes*: China: *Yunnan Province*: 3 females collected with holotype; Baoshan Prefecture: 1 female (No. 98-OP-15), pass over Gaoligongshan, Luoshuidong, 28 air km E TengChong, 24°57′N, 98°45′E, 2300m, flight trap in clearing of native forest, 26–31 October 1998, C. Griswold, D. Kavanaugh, and C-L. Long (2 paratypes deposited at the California Academy of Sciences, the rest at Hunan Normal University).

**Etymology.**—The specific name is an adjective derived from the type locality.

**Diagnosis.**—This species is similar to *Phrurolithus taiwanicus* Hayashi & Yoshida 1993 (see Kamura 2001, figs. 14–19) in having large spermathecae with separate copulatory openings and large, curved fertilization ducts, but differs in having larger spermathecae which reach the epigastric furrow.

**Description.**—Female: (Fig. 8): Carapace pear-shaped, brown-black. AER slightly recurved, PER straight in dorsal view. Cervical groove distinct and deep, head region somewhat elevated. Fovea short, longitudinal, surrounded by radiating pale pattern. Sternum heart-shaped, grayish black, paler in center, margins red brown. Chelicera weak, yellow-brown with grayish black mark dorsally, teeth small, 3 promarginal and 2 retromarginal. Palpus grayish black interrupted by grayish brown. Endites and labium grayish black, distal end pale yellow, labium longer than wide. Leg grayish brown, with paired ventral spines, Leg I, tibia with 8, metatarsus with 4, Leg II, tibia with 7, metatarsus with 3. Abdomen dorsum slightly paler than carapace, pattern yellowish gray, cardiac mark not distinct; anterior half with 3 pairs markings and 3 chevrons posteriorly; venter with gray markings: 1 pair of longitudinal striae and 2 pairs of patches. Spinnerets pale brown.

Epigynum with large ovoid atrium in posterior portion; vulva with two large spermathecae and twisted copulatory ducts with thicker anterior and thinner posterior sections (Figs. 9, 10).

Male: Unknown.

Measurements: Female (holotype): TL 4.90, CL 1.80, CW 1.50; AL 3.00, AW 2.40. Eye sizes and interdistances: AME = ALE = PME 0.09, PLE 0.10; AME–AME 0.05, AME–ALE 0.03; PME–PME 0.10, PME–PLE 0.07. MOQ L 0.29 MOQA W 0.20, MOQP W 0.30; CH 0.15, longer than AME diameter. Appendage lengths: palpus: 2.23 (0.78, 1.05, 0, 0.40); leg I: 6.46 (1.70, 2.50, 1.51, 0.75); leg II: 5.35 (1.40, 2.00, 1.20, 0.75); leg III: 4.41 (1.20, 1.51, 1.00, 0.70); leg IV: 6.60 (1.70, 2.20, 1.80, 0.90); leg formula: IV, I, II, III.

**Distribution.**—Yunnan Province, China.

### *Phrurolithus revolutus* new species
Figs. 11–16

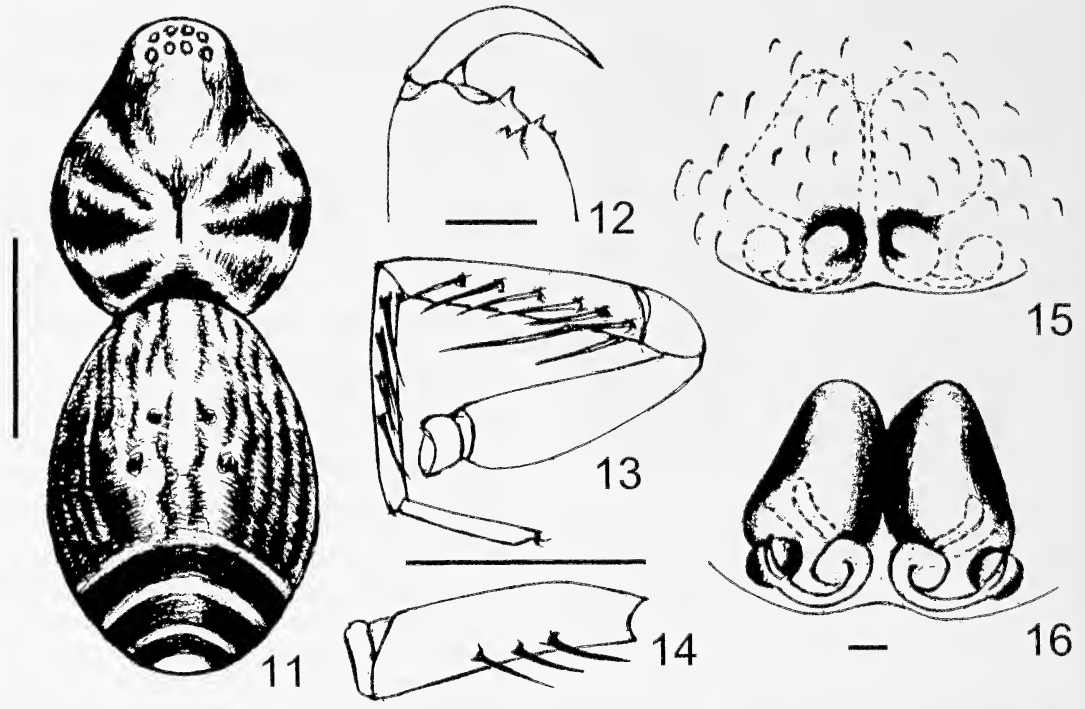
**Type material.**—Female holotype collected at 9 km ESE of Pianma (25°36′ N, 98°24′ E), Mt. Gaoligong, Yunnan Province, China, 13–18 October 1998, C. Griswold, D. Kavanaugh, and C-L. Long (deposited in Hunan Normal University, type number 98-EP-15).

**Etymology.**—The specific name refers to the curved copulatory ducts.

**Diagnosis.**—This species is similar to *Phrurolithus vulpes* (see Kamura 2001, figs. 1–7) in having large spermathecae and paired, crescent shaped copulatory openings but differs in having: 1) larger spermathecae which reach the epigastric furrow and 2) the copulatory openings more posteriorly placed.

**Description.**—Female: Carapace pale black brown, patterned with black brown. AER and PER recurved in dorsal view. Cervical groove distinct, head region slightly elevated. Carapace with distinct radial grooves, interspersed with shorter lines; fovea short, longitudinal. Sternum heart-like, grayish brown, paler in center, margins red brown. Chelicera weak, yellow-brown, with grayish brown mark dorsally, with 3 promarginal and 2 retromarginal teeth (Fig. 12.). Palpi, endites, and legs yellow-brown, femur with one grayish brown band on distal end. Tibiae I, II dark in color, with 6 pairs of ventral spines; metatarsi I, II with 4 pairs of ventral spines (Fig. 13); anterior femora with 3 prolateral spines (Fig. 14).

Abdomen dorsum iridescent with grayish black and yellow and gray patterns; cardiac mark large, pale grayish black, lined with yellow-gray margins; sides with fine longitudinal lines; posterior with 2–3 transverse bands and 1 small ellipsoid, white marking; venter median grayish black, laterally with yellow gray oblique striae; spinnerets short, yellow brown.




Figures 11–16.—*Phrurolithus revolutus*, new species, female. 11. Body, dorsal view. 12. Chelicera, retrolateral view. 13. Leg I prolateral view, showing paired ventral spines. 4. Femur II, prolateral view showing spines. 15. Epigynum. 16. Vulva. Scale bars: 11, 13, 14 = 1.00mm; 12, 15, 16 = 0.10mm.

Epigynum with atrium consisting of two small round pits near posterior margin; vulva with 2 large spermathecae and spiraled copulatory ducts (Figs. 15, 16).

Male: Unknown.

Measurements: Female (holotype): TL 3.35, CL 1.45, CW 1.05; AL 1.90, AW 1.15. Eye sizes and interdistances: AME 0.07, ALE = PLE 0.08, PME 0.55, AME–AME 0.025, AME–ALE 0.028; PME–PME 0.075, PME–PLE 0.05; MOQL 0.20, MOQA 0.14, MOQP 0.18; CH 0.075, almost equal to AME diameter. Appendage lengths: palpus: 1.50 (0.60, 0.45, 0, 0.45); leg I: 5.30 (1.35, 2.00, 1.45, 0.50); leg II: 4.42 (1.12, 1.50, 1.10, 0.70); leg III: 3.72 (1.12, 1.20, 0.90, 0.50); leg IV: 5.15 (1.50, 1.60, 1.30, 0.75); leg formula: I, IV, II, III.

**Distribution.**—Yunnan Province, China.

## ACKNOWLEDGMENTS

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# THE MOVEMENT AND ACTIVITY PATTERNS OF SIMILAR-SIZED ADULT AND JUVENILE CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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**ABSTRACT.** Adult male animals are commonly believed to exhibit higher activity than other conspecifics, but little information exists to compare their activity with that of other conspecifics of similar size. Here we compare the activity of adult male and similar-sized juvenile female crab spiders *Misumena vatia* (Araneae, Thomisidae). Adult males moved farther and more frequently than juvenile females of similar size (fourth instar) that were not affected by impending molt. Juvenile females influenced by impending or recent molt did not move as far or as frequently as nonmolting juveniles, even though their exoskeletons were hard enough to permit rapid movement. A small sample of penultimate males, of similar size to the adult males and juvenile females, exhibited activity patterns similar to the juvenile females. All of these data indicate that the high activity level of adult males is not a simple manifestation of behavior that is solely a function of size. We suggest that the high activity levels of the adult males facilitate search for scarce, cryptic mates.

**Keywords:** Activity level, molt, sit-and-wait predator

The high level of activity commonly attributed to reproductively active adult male animals is typically associated with searching for fertile females, a trait likely to enhance reproductive success by increasing contact with females (Thornhill & Alcock 1983; Andersson 1994). Seldom, however, is it explicitly established whether these perceived high activity levels of the males are unique to them.

Hypothetically, the size differences of juvenile and adult animals could by themselves account for their respective levels of activity. Adults of many species considerably exceed the size of younger individuals. However, one way to control the effect of size on activity is to compare the activity of different categories of a species that reach similar sizes (in this instance, adult males, juvenile females, and penultimate males). Size relationships such as the one considered here occur in species characterized by small adult males and large, relatively immobile adult females. In these systems, scramble competition for finding virgin females (Ghiselin 1974; Parker 2000) may result in high levels of activity by males, potentially driven by sexual selection.

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The crab spider *Misumena vatia* (Clerck 1757) (Thomisidae) is an excellent species for addressing how activity rates vary over the life cycle. It is a sit-and-wait predator that hunts on flowers for visiting insect prey (Morse 1979; Morse & Fritz 1982). Males are tiny in relation to adult females, at times no more than 1% of the mass of gravid adult females (Gabritschevsky 1927; LeGrand & Morse 2000). Thus, they provide an opportunity to compare the activity of adult males with juvenile females of similar size. Although sit-and-wait predators, adult males have shorter giving-up times on hunting sites than adult females, penultimate females (both larger), or penultimate males (similar size) (Morse & Fritz 1982; Chien & Morse 1998; LeGrand & Morse 2000).

The difference in activity between adult females and adult males could be merely a consequence of the large adult females becoming less mobile than the earlier instars, or adult males becoming more active or both. Given the likely pressures of scramble competition, with adult male movement focused on finding virgin females (Vollrath & Parker 1992; Kotiaho et al. 1998), we predicted that adult

males would move more rapidly (number of moves and distance per unit time) than other life-cycle stages. Since they often do not detect sexually mature females at distances exceeding 5 cm (Holdsworth & Morse 2000), male *M. vatia* should experience especially strong selection to move rapidly, thereby maximizing their number of visits to sites potentially occupied by these females (LeGrand & Morse 2000; Anderson & Morse 2001). Here we make the more critical comparison by testing the hypothesis that adult males are more active than other similar-sized conspecifics; i. e., fourth-instar females. We also test whether any such differences involve frequency of moves or length of moves. To obtain the appropriate data, we developed a practical method for quantitatively describing movement and activity levels of these spiders.

Like all arthropods, spiders spend most of their lives encased in jointed, chitinous exoskeletons, structures that provide protection and prevent desiccation. However, aside from their soft abdomen, spiders cannot increase in size except by molting, a state that profoundly affects activity and movement (Foelix 1996). Since *M. vatia* molt frequently (Gabritschevsky 1927), it was necessary to establish unequivocally whether the juveniles under study were influenced by impending molt, which could only be accomplished after establishing when an individual molted. It was thus also necessary to test the juveniles at both intermolt and molt periods, and we consequently present these results and comment upon them as well.

Voucher specimens of *Misumena vatia* have been deposited in the American Museum of Natural History.

## METHODS

**Study site and study organisms.**—We conducted this study at the Darling Marine Center in South Bristol, Lincoln County, Maine. We performed all trials during June–August of 1998 and 1999 in a 3.5 ha field that is mown yearly in October.

*Misumena vatia* occur naturally at the study site and in surrounding fields and roadsides, spending most of their time in the herbaceous vegetation above 20 cm. They typically course through the fields, moving through most of the vegetation relatively quickly, but remaining on flowers, which they use for hunting sites, for considerably longer periods (Morse & Fritz 1982; LeGrand & Morse 2000). We used juvenile females comparable in size to the adult males. Other than being qualitatively sized by eye, they were randomly collected. We collected the *M. vatia* used in this study along roadsides adjacent to the study area. We recorded mass, carapace width, and length of leg 1 of each individual at capture. We also noted when a juvenile spider molted and took its new measurements. Except during measurements and behavioral trials, spiders were maintained individually in 7 dram clear plastic vials (5 cm tall, 3 cm diameter) and fed mosquitoes, flies and small moths every third day.

**Movement and activity.**—We observed both free-ranging spiders in the field and also monitored spiders in activity cages set in the field. Cages were 30 × 30 × 30 cm and covered on all sides, including the bottom, with dark green polyester mesh (8 × 10 mesh fibers/cm$^2$). We ran all trials in the field in clear weather during daytime hours, the time at which the majority of *M. vatia*'s activity occurs (Morse 1979; Morse & Fritz 1982).

In initial free-ranging trials we placed a focal spider on a stem of grass approximately 20 cm above the ground. To avoid sites that would slow spider movement, we ran all trials where no flowers were present, thus allowing us to record maximum searching capability, rather than movement confounded with extended visits to flowers. This measure should indicate the maximum distance the spiders would move over a unit of time and should also reflect their ability to locate a favored hunting site or object, be it a flower or a female. Following a 5 min acclimation period, free-range trials lasted 1 h, with activity and location recorded every 5 min, for a total of 12 observation times per individual. Depending upon the spider's position and activity at the instant of recording, five categories of activity were recognized: A). location changed since previous observation, in motion at moment observed (either traveling or changing orientation); B). location unchanged, but changing orientation at moment observed; C). location changed since last observation, but stationary; D). location unchanged, but orientation changed; E). neither location nor orientation changed, stationary. (Categories B, D and E cannot exclude the possibility that a spi-

der has changed its location but then returned to it.)

We had originally intended to invest most of our efforts in measuring free-ranging individuals in the field. However, it quickly became apparent that we were losing so many individuals in the open field tests that it was extremely difficult to obtain complete runs of adult males before losing them. In particular, we frequently lost the small agile males in the vegetation and litter in spite of our best efforts to monitor them. Further, individuals lost prematurely usually moved more rapidly than those followed for an hour. Given the small sample available, it was not practical to run any of the penultimate males in the open field. The multiple runs needed to ascertain the molt stage of the juvenile females were also impractical because of the danger of losing them during one of these runs.

We thus gave up the efforts to measure free-ranging individuals in the field and concentrated on running cage trials. This technique provided a standardized substrate for measuring movement, thereby permitting direct comparison between individuals and between trials. The cages allowed us to eliminate hunting sites that would prevent accurate measurement of maximum activity levels. Most importantly, they eliminated the loss of male spiders. We used the same activity categories and times for individuals in the cage trials as for the field trials.

We positioned each cage in the open, directly on the ground, and transferred the spider from its vial to the middle of the mesh bottom of the cage. Positions of the spiders were determined with a millimeter rule, orientation noted, and changes measured and recorded at each 5 min interval. We thoroughly scrubbed the mesh and rotated the cages between runs to eliminate any possible position effects. Since exhaustive experiments have revealed no effect of pheromones on lines or in the air (Anderson & Morse 2001), we did not further control for this factor. We ran a maximum of four cage trials simultaneously, staggering the start by 1 min per cage.

**Condition of nonmolting and molting individuals.**—We divided the runs of the juvenile females into those affected by molts and those made at intermolt intervals. Molt periods encompassed the time when the integument commenced to break down, leading up to the molt, through the time when the integument of the next instar had completely hardened. Premolting changes can often be detected as parts of the integument begin to take on a somewhat transparent, vacuolated appearance, the start of the breakdown of the old integument. This change begins 4–5 d before molt (Foelix 1996); we therefore selected, a priori, the period from 5 d before molt to 1 d after molt as the "molting period", and the rest of the time as the "nonmolting period". Runs were performed independently of these periods, since we could only make the above-noted separation into nonmolting and molting condition after recording ecdysis. Tests on molting days were run only after the carapace had hardened enough so that the spiders were able to move about readily. All penultimate males had to be tested similarly to the females, and it was the failure of most of these individuals to remain in a nonmolting state over 5 d that resulted in the small sample size.

**Analysis.**—Each adult male and penultimate male contributed one activity trial to the analysis. Several juveniles contributed two trials, one as a "nonmolter" and one as a "molter". Juveniles were tested daily to determine when they could be incorporated into nonmolting and molting categories. Molting individuals were categorized as those between 5 d pre-ecdysis and one day post-ecdysis, following Foelix (1996). Only the first nonmolting run and first molting run were used for the analyses.

We obtained a measure of total activity for each individual: the number of 5 min periods in which an individual's activity warranted designation of Category A, B, C or D. A maximum performance would be 12, a score of 1 being assigned for each of the 5 min observation periods in which movement took place during an hour (Category A, B, C or D). We also calculated a high activity measure (number of Category A movements only) for the cage trials. We reasoned that individuals travelling at observation times likely moved more often than those whose positions changed, but were not observed in transit at observation times. We measured movement by summing the distances between an individual's locations on consecutively occupied sites. This measure gives a minimal possible distance traveled by the spiders; distances traversed during reversals of direction or roundabout

Table 1.—Total activity scores and distances (± SE) moved by free-ranging spiders.

| Group | $n$ | Activity score | Distance |
|---|---|---|---|
| Adult male | 12 | 8.4 ± 0.58 | 197.9 ± 62.87 |
| Juvenile female | 10 | 7.0 ± 0.85 | 117.8 ± 25.46 |

circuits within a single observational period would not be recorded.

## RESULTS

**Mass and body dimensions.**—Adult males ($n$ = 32) weighed 5.2 ± 0.25 mg ($x$ ± SE) when captured, with carapaces 1.4 ± 0.03 mm wide and legs 6.3 ± 0.13 mm long. Mass was positively correlated with carapace width ($r$ = 0.690, $P < 0.001$, one-tailed product-moment correlation), and leg length ($r$ = 0.373, $P <$ 0.05, same test). Carapace width and leg length were also positively correlated ($r$ = 0.549, $P < 0.01$, same test). Sequential Bonferroni tests (Rice 1989) were applied to all of the correlations presented in this section.

The juveniles ($n$ = 38) weighed 5.2 ± 0.40 mg and measured 1.3 ± 0.04 mm in carapace width and 4.9 ± 0.22 mm in leg length. Mass was positively correlated with carapace width ($r$ = 0.743, $P < 0.001$, same test) and leg length ($r$ = 0.713, $P < 0.001$, same test). Carapace width and leg length were positively correlated ($r$ = 0.843, $P < 0.001$, same test). Males and females used in these experiments did not differ significantly in either mass ($t$ = 0.090, $P > 0.9$) or carapace width ($t$ = 0.287, $P > 0.5$), but did differ in limb length ($t$ = 4.324, $P < 0.001$), all in two-tailed $t$-tests. Thus, males had longer legs than females of similar size.

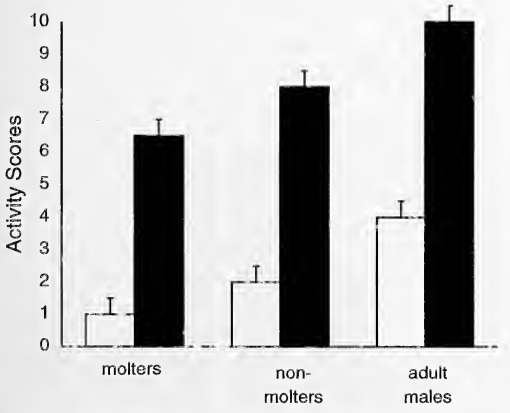


Figure 1.—Activity levels ± SD for adult males ($n$ = 32), nonmolting juvenile females ($n$ = 38), and molting juvenile females ($n$ = 20). Black bars = total activity, white bars = high activity.

**Free-ranging trials.**—We present the data on free-ranging trials to illustrate the difficulty of obtaining velocity measures of adult males in the field and to justify our resort to the cage trials. In the free-ranging trials (Table 1), total activity scores of the adult males did not differ significantly from those of nonmolting juvenile females ($U$ = 35.5, $Z$ = 1.315, $P > 0.05$, one-tailed Mann-Whitney $U$-test). Neither did the distance traveled differ significantly between the two groups ($U$ = 38, $Z$ = 1.137, $P > 0.1$, same test). However, since both mean activity and mean total distance traveled by the adult males considerably exceeded those of the juvenile females (Table 1), the nonsignificant levels were likely a consequence of the especially high variance of the field individuals. Additionally, several rapidly moving males were lost in the field before adequate information could be gathered from them for a measurement. These results prompted our effort to design a method that would eliminate the losses of experimental subjects and that would decrease variance due to likely artifacts.

**Cage trials.**—Adult males were significantly more active (total activity scores) than nonmolting juvenile females ($U$ = 394.5, $n$ = 32, 38; $Z$ = 2.517; $P < 0.02$, one-tailed Mann-Whitney $U$-test), and the difference in high activity scores between the two groups was particularly large ($U$ = 229.5, $Z$ = 4.462, $P < 0.0001$, same test) (Fig. 1). Adult males also moved greater distances than nonmolting juvenile females ($U$ = 380, $Z$ = 2.688, $P <$ 0.01, same test) (Fig. 2), a consequence of making both longer and more frequent moves (Figs. 1 & 2). We have not compared the contributions of these two variables statistically, because they are unlikely to be independent of each other.

Five penultimate males that fit the molting criteria (did not molt for 5 d following a run)

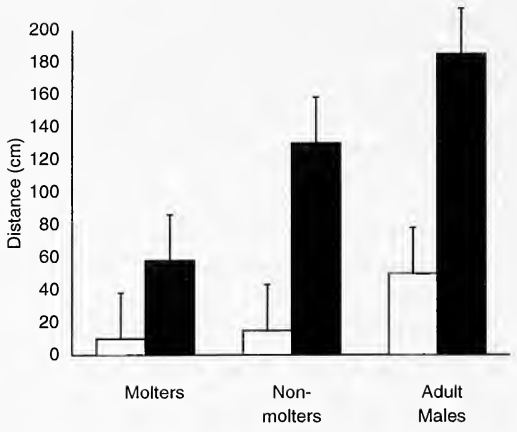


Figure 2.—Total distance moved (minimum/h) ± SD and mean lengths of single moves in cage trials by adult males, nonmolting juvenile females, and molting juvenile females. Black bars = total distance, white bars = mean length of single moves.

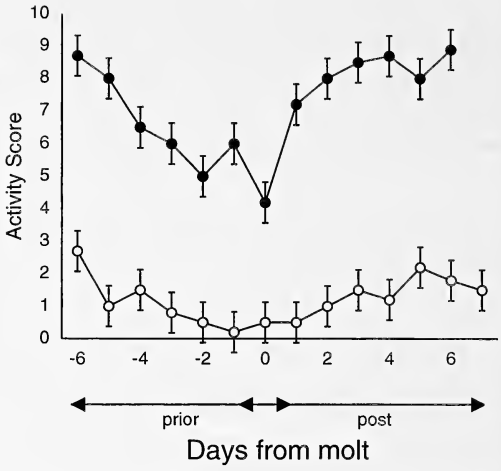


Figure 3.—Activity levels (total activity in black, high activity in white ± SD) of juveniles across a molting period. Days from molt depicted on horizontal axis such that 0 = molt day. Each point represents mean activity (± SD) of trials on molt day or specific number of days before or after molt.

exhibited activity levels similar to those of nonmolting juvenile females (total activity score = 6.3 ± 1.9; high activity score = 2.3 ± 1.0) ($U = 79$, $Z = 0.001$, $P > 0.9$; $U = 74.5$, $Z = 0.001$, $P > 0.9$ in two-tailed Mann-Whitney $U$-tests). We obtained no data on distance moved from these individuals. On the basis of these few individuals it thus does not appear that the adult male—juvenile female differences in activity we have reported are solely a consequence of the sex in question.

**Activity near the molt.**—In the process of establishing the molting state of juvenile females, we obtained considerable information about the activity levels of individuals in molting as well as nonmolting condition. These spiders exhibited a strong relationship between activity level and time before molt (Fig. 3). Both total activity and high activity scores dropped prior to molt, with a rapid return following ecdysis. The total activity score was lowest for individuals tested on their actual day of molt; the high activity score reached its minimum one day prior to molting (Fig. 3). None of the measurements included individuals with a nonfunctionally soft exoskeleton. Movements of individuals during molt and nonmolt periods differed significantly in total activity (Fig. 1: $T = 20$, $n = 20$, $Z = 3.546$, $P < 0.001$, one-tailed Wilcoxon matched pairs signed ranks test), high activity (Fig. 1: $T = 32$, $Z = 2.330$, $P < 0.02$, same test, and total distance traveled (Fig. 2: $T = 15$, $Z = 3.733$, $P < 0.001$, same test). This difference is a consequence of both the length and number of moves made by these individuals (Figs. 1 & 2).

The mean intermolt period was 20.6 ± 6.6 d (Fig. 4). Given a molt phase of approximately 6 d, a juvenile crab spider spent about one-third of its juvenile life in a molt phase, and about one-third of the juveniles were thus in a molt phase at any given time. The length of an instar did not correlate significantly with size (carapace width) ($T = 47$, $n = 14$, $Z = 0.345$, $P > 0.7$, two-tailed Wilcoxon matched pairs signed ranks test), nor did instar length

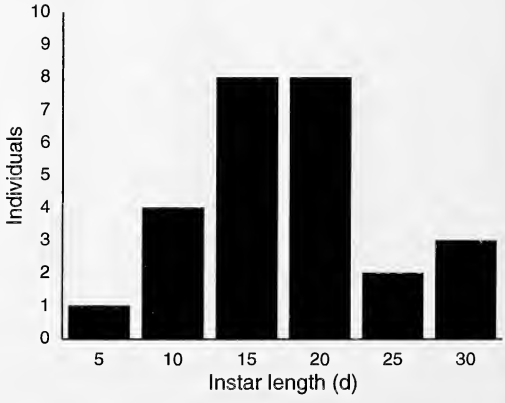


Figure 4.—Frequency distribution of time in days (d) between molts of juveniles.

correlate with the percentage of increase in size achieved via molt ($T = 43$, $n = 14$, $Z = 0.534$, $P > 0.5$, same test) or length of the preceding instar ($T = 19$, $n = 8$, $Z = 0.140$, $P > 0.8$, same test).

## DISCUSSION

Animals with long, slender legs are often cursorial. Therefore, LeGrand & Morse (2000) hypothesized that, given the differences between juvenile females and penultimate males, the long legs of adult males facilitate rapid movement. In fact, the adult males in this study made significantly longer moves than did juvenile females. However, a substantial part of the difference between adult males and the other groups lay in the frequency of their moves, especially high-activity moves, rather than simply in the length of their moves. Thus, the difference in adult male movement cannot be attributed solely to differences in the shape of their legs.

Although one might argue that the cages provided an unnatural environment in which to run the experiments, the distances traveled by the spiders in the cages and in the open were similar (though less variable). The cages also exposed all of the spiders to the same conditions and cues. We therefore conclude that the cage trials served as an adequate estimate of movement rates of the different age and sex categories of these spiders in the field.

Innate behavioral factors might dictate the initiation of movements, as seen in the initiation of other behavioral patterns (Morse 2000) of *M. vatia*, but physiological mechanisms may dictate the length of the movements in part. Since spiders are physiologically severely limited in their ability to generate aerobic activity (Linzen & Gallowitz 1975; Anderson & Prestwich 1982), the adult males may avoid severe oxygen debts by restricting the lengths of their movements to the modest ranges observed, even though they exceeded those of the juvenile females. Even highly cursorial wolf spiders (Lycosidae) have tightly constrained sprint distances (Bristowe 1939; Morse 1997).

In other spiders investigated, females usually release pheromones prior to mating (e. g., Tietjen & Rovner 1982; Fernández-Montraveta & Ruano-Bellido 2000), behavior that attracts males, as a result of following lines "scented" with pheromones or, possibly, by airborne pheromones (Searcy et al. 1999). However, adult male *M. vatia* only detect females within a limited range of a few cm (LeGrand & Morse 2000) and follow draglines somewhat indiscriminately (Anderson & Morse 2001). Although the females are capable of mating immediately following molt (Holdsworth & Morse 2000), adult females in our populations on average were not mated until two to three days after molting, probably because, in the apparent absence of cues, the males could not locate them quickly (LeGrand & Morse 2000). The two-three day hiatus between molt and mating suggests that sizeable reproductive opportunities may be available to agile individuals. Therefore, males should be under extremely strong selective pressure to move frequently, quickly, and efficiently in order to find females. The high activity levels of the males should facilitate search for these cryptic females.

We initially planned extensive comparisons between adult males and penultimate males, which are of similar size, but penultimate males were available in the field for only limited periods in both the autumn and spring. We did not run them in the autumn out of concern that impending diapause might bias the results (Tauber et al. 1986; Tanaka 1992). In the spring most penultimate males molted within five days of their initial test and thus could not be used for this comparison, since before certifying a run for use in the analysis we had to establish that they were in a nonmolting state. The results from the small sample agree with the more general earlier findings of activity among penultimate males (LeGrand & Morse 2000) and strengthen the conclusion that the unique rates of adult male movement are not a mere consequence of sex, but are related directly to male maturation.

Juveniles 5 d prior to molt through 1 d after molt were significantly less active than nonmolting juveniles of the same size, whether using activity scores or distance traveled as criteria. Spiders tend to withdraw from sight and refuse prey for up to nearly a week prior to ecdysis (Foelix 1996). The initial decrease in activity of molting juveniles was probably a consequence of the onset of apolysis (separation of the new epidermis from the old cuticle). The commencement of apolysis is difficult to predict, but may precede ecdysis by

up to a week in insects and spiders (Wigglesworth 1984; Foelix 1996). Differences in activity between molting and nonmolting juveniles resulted both from the molters moving less frequently and exhibiting far less high-activity behavior than nonmolting individuals. In contrast, the greatest difference between adult males and both molting and nonmolting females lay in the large amount of high-activity behavior in the adult males. Molting-condition juveniles thus exhibit severely constrained activity levels, which result in large part from a decline in the number of moves they make, rather than the length of moves. It must be emphasized that this low level of activity is not a consequence of a physical inability to move, since the period of forced inactivity resulting from a soft exoskeleton constitutes only several hours of the six-day period of low activity.

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# THE SYSTEMATICS OF THE *EREMOBATES SCABER* SPECIES-GROUP (SOLIFUGAE, EREMOBATIDAE)

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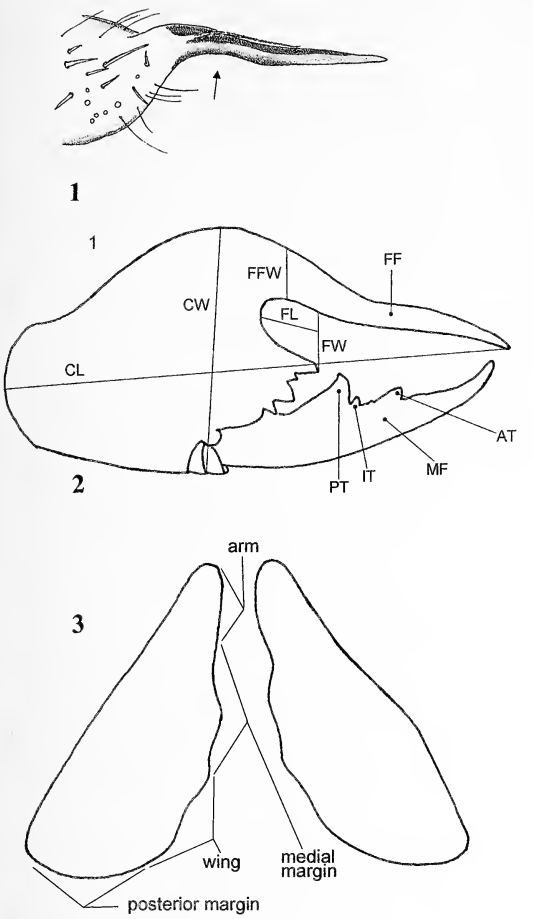
**ABSTRACT.** The scaber group of the genus *Eremobates* is reviewed in terms of new characters and a more restricted biogeographic area. Three new species are described from the U.S.A.: *Eremobates socal* (California), *E. icenoglei* (California), *E. corpink* (Utah). We synonymize *E. gladiolus* Muma with *E. scaber* (Kraepelin); *E. consors* Muma, *E. ascopulatus* Muma and *E. flavus* with *E. ascopulatus* Muma; and *E. mimbrenus* Muma with *E. mormonus* (Roewer). *Eremobates scaber*, *E. hodai* Muma, *E. clarus* Muma, *E. similis* Muma are now described from both sexes. All scaber species except the Mexican species, *E. legalis* Harvey, are now known from both sexes. We also present the first phylogeny of the species group based on morphological characters. This phylogeny demonstrates a geographic grouping into northern and southern clades.

**Keywords:** Solifugids, phylogeny, cladistic analysis, biogeography

Muma (1951) redescribed the genus *Eremobates* Banks 1900 to include those solifugid species characterized by males with a basally dilated mesoventral groove running the length of the mesodorsal or mesoventral surface of the fixed finger. The male flagellum complex consists of dorsal striate setae, ventral striate setae, and a flattened apical plumose seta covering much of the mesoventral groove. The female genital opercula varied depending upon the species-group. Additionally the *Eremobates scaber* species group was erected by Muma (1951) to include those *Eremobates* whose males were characterized by a broad basal notch occupying one-third or more of the length of the fixed finger in dorsal view (Fig. 1). In the scaber group the mesoventral groove is deep and narrow. The female genital opercula are roughly triangular with species distinguished by differences in the medial margins.

Muma (1951) listed six species in the scaber group including the typical or defining species *E. scaber* (Kraepelin 1899) although he had not seen the female type specimen. After examining type specimens in both the U.S. and Europe as well as other specimens from various collections and collectors Muma (1970) recalled Kraepelin's 1899 description of *Datames scaber* based on the female type from "Washington Territory" as the correct characterization of *Eremobates scaber*. He used his 1951 description, erroneously attributed to *E. scaber*, to establish *E. septentrionis* Muma 1970, used his 1951 description of *E. geniculatus* to erect *E. mormonus* (Roewer 1934) and defined *E. geniculatus* (C.L. Koch 1842) (Simon 1879, misidentified) using Simon's 1879 description of a single female from Mexico (Muma 1970). In 1989 Muma described six new species. This resulted in 15 species in the scaber group with *E. scaber*, *E. actenidia* Muma 1988, *E. clarus* Muma 1989, *E. consors* Muma 1989, *E. ascopulatus* Muma 1951 and *E. hodai* Muma 1989 described from only one sex although Muma included the male of *E. scaber* in the key. *Eremobates clarus*, *E. actenidia* and *E. consors* were each described from a single specimen and *E. ascopulatus* from two males. *Eremobates similis* (Muma 1951) was noted as being described in both sexes (Muma 1989), but the female description has not been found.

In describing *E. scaber*, Muma (1951) used specimens from an area that extended from the northwestern United States to Las Vegas, Nevada but noted that it might include other species of this group. In addition, other species of this group seemed to have sympatric ranges (Muma 1951, 1962, 1989). In each of




Figures 1–3.—Diagnostics used in compiling data for scaber group. 1. *Eremobates scaber*, dorsal view of male fixed finger (arrow identifies basal notch). 2. Diagram of male chelicera showing ranges of measurement and morphological characters: CL = cheliceral length, CW = cheliceral width, FL = fond length, FW = fond width, FFW = fixed finger width, FF = fixed finger, MF = movable finger, PT = primary tooth, IT = intermediate tooth, AT = anterior tooth. 3. Diagram of female genital operculum.

his publications Muma (1951, 1962, 1989) cited several problems with the distinction between species and problems of sympatric associations. Muma (pers. comm.) indicated that this group needed to be more thoroughly studied.

For the most part, this group is an inhabitant of piñon pine-juniper or desert shrub communities. Muma (1963) identified *E. zinni* (Muma 1951), *E. similis*, *E. ctenidiellus* and *E. mormonus* as inhabitants of the Mercury, Nevada Nuclear Test Site, a Mojave Desert region, although some of the specimens were misidentified. Allred & Muma (1971) listed *E. septentrionis* and *E. ctenidiellus* as inhabitants of the Snake River Plain which is part of the Columbian Plateau. Brookhart (1972) found *E. mormonus*, later changed to *E. similis*, in the San Luis Valley of Colorado and *E. ctenidiellus* in the mesa regions of western Colorado. The Sevilleta Long Term Ecological Reserve project at the northern tip of the Chihuahuan Desert surveyed six distinct desert grassland/high desert areas and found *E. similis* in only the piñon-juniper association (Brookhart & Brantely 2000). At the Hanford Nuclear Site, Rich Zack's *E. scaber* material (WSU) was collected in Great Basin Desert shrub habitat, and various Canadian specimens were collected in the sagebrush of the Okanogon Valley. *Eremobates scaber* group species have been collected at 2394 m in Wyoming, 2303 m in the San Luis Valley of Colorado, and on Mt. Palomar, California.

Muma (1951, 1962, 1970, 1989) used length vs. width of the fondal notch, number and shape of ctenidia, and number of palpal papillae, as well as coloration of appendages to separate each species. The number of ctenidia ranged from 0–6. The palpal scopula varied from none to over 120 papillae. Females were identified by the structure of the genital operculum and the coloration of appendages. Coloration of eye tubercle and malleoli were noted but were consistently the same for all species with eye tubercles dark and malleoli white. Abdominal coloration varied from a pale yellow to a grey background dorsally and ventrally with lighter pleural membranes between species and also between specimens of the same species. Many specimens had tergites with a rectangular, brownish, violet pigmentation which gave the appearance of a broad stripe to many specimens. Muma (1951) calls this a sclerite although it is not particularly thick or hardened. It was not found to be diagnostic in this study.

Male chelicerae have no teeth on the fixed finger and some variation in the shape of the fixed finger in ectal view. The movable finger follows the general pattern of a large primary tooth, two intermediate teeth, the posterior being larger and an anterior tooth. The mesal tooth varies from tiny to absent. Female chelicerae have a fixed finger with teeth ordered successively posterior to anterior, intermedi-

ate tooth, large primary tooth, two intermediate teeth, medial tooth, a single intermediate tooth and a smaller anterior tooth. The female movable finger has a large primary tooth, a variable sized anterior tooth and two intermediate teeth, the posterior of which is larger. The mesal tooth varies from absent to medium size. Fondal teeth in both male and female grade out I, III, II, IV in size, although in some species the fondal tooth III is equal in size to fondal tooth I. Due to wear, the intermediate teeth on both male and female movable fingers are sometimes hard to diagnose.

## METHODS

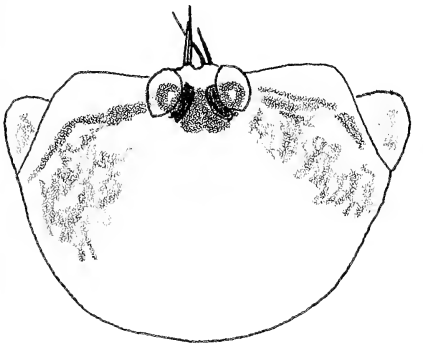
Because of their nocturnal habits solifugids are usually not collected in abundance and study specimens are difficult to obtain (Muma 1951, 1970, 1989; Punzo 1998). Efforts were made to accumulate at least five males and five females from identifiable geographical regions. The Sevilleta Long Term Ecological Research (LTER) site provided specimens over a seven year period (Brookhart & Brantley 2000) that enabled us to identify variations within an isolated species population. Brookhart conducted limited pitfall projects in the San Luis Valley, the northwest corner of Colorado near Dinosaur National Monument and the area around Colorado National Monument on the Colorado Plateau from 1997–1999. He also collected from southeast Utah using the same method during 2000–2001. A one year pitfall series from Hanford Site, Benton County, Washington collected by Rich Zack et al. was also examined. Collections from other institutions were also provided for study. We were able to examine all of the types. Coordinates for some specimens are approximate as they are based on historical locale information. We determined collection coordinates for specimens post hoc when possible. However, if the specimen was collected 6 km or more from the given site, the coordinates were not reported since the locale information on the collection label was considered too vague.

Using the methods of Muma (1951), Brookhart & Muma (1981, 1987) and Muma & Brookhart (1988) we measured the length of palpus, leg I, leg IV; length and width of chelicera and propeltidium; length and width of fondal notch; and width of base of fixed finger. Fig. 2 indicates measurement areas. Abbreviations used to indicate various cheliceral structures are as follows: FF = fixed finger; MF = movable finger; PT = primary tooth; AT = anterior tooth; MT = medial tooth; IT = intermediate tooth; MST = mesal tooth. No satisfactory measurement of the depth of the notch could be found but depth could be inferred based on the amount of "crimping" or upturn of the male fixed finger. Those with a deeper notch demonstrated a more deeply crimped aspect when viewed ectally (see ectal view of *E. scaber*, Fig. 31). Female length; length of palpus, Leg I, Leg IV; length and width of chelicera, propeltidium and genital operculum were also made. All measurements are in millimeters.

The number, shape, and relative length of ctenidia to succeeding tergite was noted. Counts were made of palpal papillae. Color of palpus, legs I, II, III, IV and general overall color especially that of the propeltidium was recorded. The shape of the female genital operculum especially the medial margin was observed using some new terminology (see Fig. 3).

In addition to previously utilized characters, the shape of the anterior tooth of the male fixed finger, the absence or presence of a cleft anterior to the anterior tooth on both male and female cheliceral movable fingers, the presence and size of the mesal tooth, the position of the posterior intermediate tooth on the principal tooth of the male and female movable finger were analyzed. We investigated the Ectal Cheliceral Cluster Setae (ECCS) of Muma (1985) but found no useful parameters.

Ratios used previously by Muma (1951, 1970, 1989), Brookhart & Muma (1981, 1987), Muma & Brookhart (1988), and Brookhart & Cushing (2002) were computed. These ratios are as follows: A/CP = the sum of the lengths of palpus, leg I, and leg IV divided by the sum of length of chelicera and propeltidium indicating length of appendages in relation to body size. The larger the number, the longer legged is the species. FL/FW indicates whether the chelicera fondal notch is longer or wider. Longer is defined as the anterior to posterior axis and width is defined as the dorsal to ventral axis. FW/FFW diagnoses the size of fondal notch compared to



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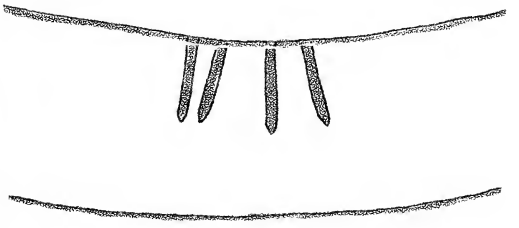

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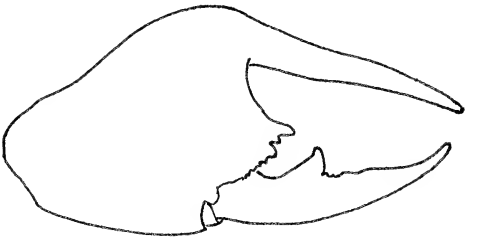

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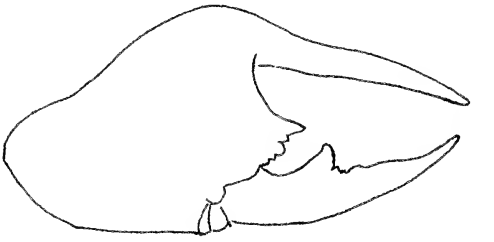

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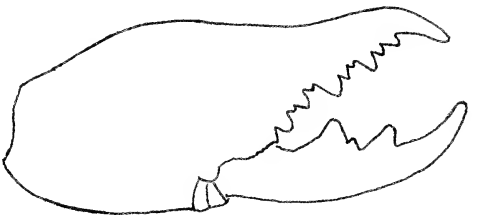

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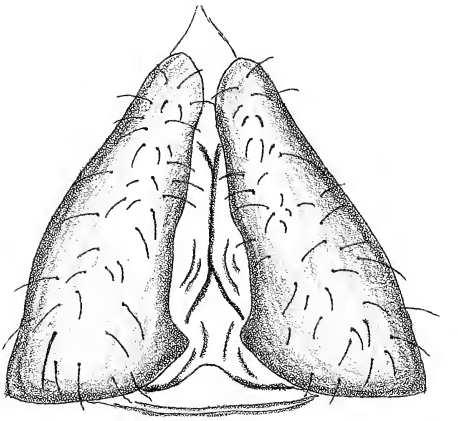

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Figures 4–9.—*Eremobates icenoglei*, new species. 4. Dorsal view male propeltidium. 5. Ectal view male right chelicera. 6. Mesal view male right chelicera. 7. Ventral view male ctenidia. 8. Ectal view female right chelicera. 9. Ventral view female genital operculum. Scale lines = 1 mm.

the thickness of fixed finger. CW/FFW is used to indicate whether the fixed chelicera finger is thin or robust in relation to the size of the chelicera. GOL/GOW demonstrates the relative size of the female genital operculum in terms of length and width.

Because of limited and unequal sample size the Tukey-Kramer Analysis of Variance (ANOVA) was used to test differences in ratio means of each population as recommended by Sokal and Rohlf (1981). New parameters are given whenever possible for both males and females since Muma's measurements were sometimes based on a few specimens and from widely separated localities suggesting that more than one species might be included. We attempted to use specimens representative of a given species from a defined geographic province since it appeared that there was no sympatric association except in the Nevada Test Site area where *E. zinni* and *E. ascopulatus* appear to be sympatric.

Over 250 specimens were used in this study, many more than were available to other investigators. We describe the male of *E. scaber* and the females of *E. clarus*, *E. similis*, *E. actenidia* and *E. hodai*. Every species except *E. legalis* Harvey 2002 is now known from both sexes and a reduced and more specific geographic range for each implied.

The following institutions have loaned us types and specimens for observations: American Museum of Natural History (AMNH), Norm Platnick; Athabasca University (ABU), Robert Holmberg; Brigham Young University (BYU), Richard Bauman; California Academy of Science (CAS), Charles Griswold; Colorado State University (CSU), Boris Kondratieff; University of Colorado at Boulder (CU), Virginia Scott; Florida State Collection of Arthropods (FSCA), G.B. Edwards and Paul Skelly; University of New Mexico Museum of Southwestern Biology, Sandy Brantley; Utah State University (USU), Wilford Hansen; State of Idaho Dept. of Environmental Quality (ID), W.H. Clark; Spencer Museum, University of British Columbia, Vancouver (SMUBC); Royal British Columbia Museum, Victoria (RBCM); Royal Ontario Museum, Toronto (ROM); Washington State University James Entomological Collection (WSU), Richard Zack; Museum National d'Histoire Naturalle, Paris, France (MNHN), Christine Rollard.

## SYSTEMATICS

### Family Eremobatidae Kraeplin
### Genus *Eremobates* Banks 1900

*Datames* Simon 1879:113 (preoccupied).
*Datames scaber* Kraepelin 1899.
*Eremobates* Banks 1900:426 (new name for *Datames* Simon).
*Eremoperna* Roewer 1934:557 (in part).
*Eremopus* Roewer 1934:561 (in part).
*Eremognatha* Roewer 1934:566 (in part).
*Eremocosta* Roewer 1934:569 (in part).
*Eremostata* Roewer 1934:571 (in part).

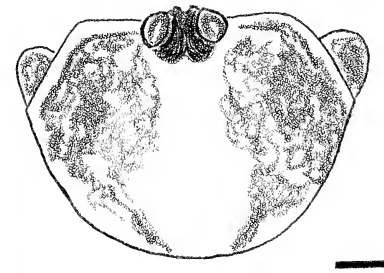
**Type species.**—*Gluvia cinerascens* E.L. Koch 1842 (junior synonym of *Galeodes pallipes* Say 1923). Muma (1951) described the genus *Eremobates* as small to medium sized Eremobatidae with a mesoventral groove that extends the entire length of the male fixed finger. The flagellum complex is composed of a dorsal row of simple tubular bristles that are sometimes striate and a ventral row of S-shaped, flattened, plumose bristles that form an arch over the basal third of the mesoventral groove. The apical, plumose bristle of the ventral row is straight and forms a parallel covering over the apical two-thirds of the mesoventral groove. The first post-spiracular abdominal sternite of males are with or without ctenidia. Genital operculum of female variable. This description did not change in later works (Muma 1962, 1970, 1989).

### *Eremobates scaber* (Kraepelin 1901)
### Figs. 31, 42, 47, 52

*Datames scaber* Kraepelin 1899:243, fig. 19f.
*Eremobates scaber* (Kraepelin 1899), Kraepelin 1901:124–125, fig. 91; Muma 1970:12, fig. 10; Muma 1989:8—9.
*Eremostata scabra* (Kraepelin), Roewer 1934:124.
*Eremobates gladiolus* Muma 1951:57–58, figs. 58–60; Muma 1970:11–12; Muma 1989:9. NEW SYNONYMY.

**Type.**—Female holotype of *Datames scaber* No. 9137, from "Washington Territory", US in the E. Simon collection, Paris, France (MNHN). Male holotype of *Eremobates gladiolus* from Maupin, Wasco County, Oregon, US (45°11′N, 121°04′W), 19 July 1934, J.M. Pearson, in AMNH. Female allotype from Starbuck, Columbia County, Washington, US (46°31′N, 118°07′W), 4 July 1938, C.S. Brenner, in AMNH.

**Diagnosis.**—Males: Most easily identified by the strongly upturned or "crimped" por-



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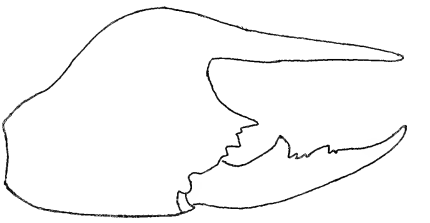

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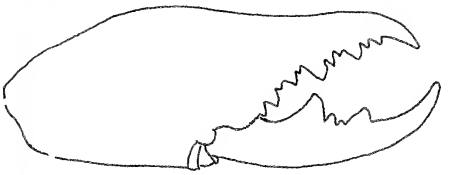

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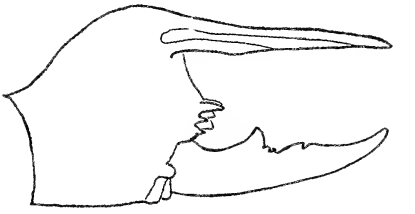

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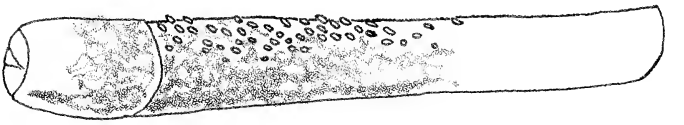

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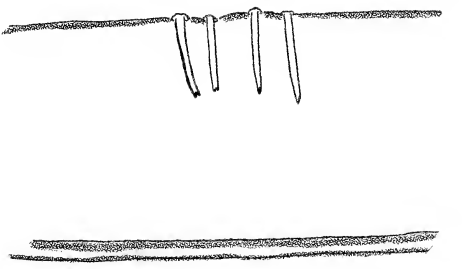

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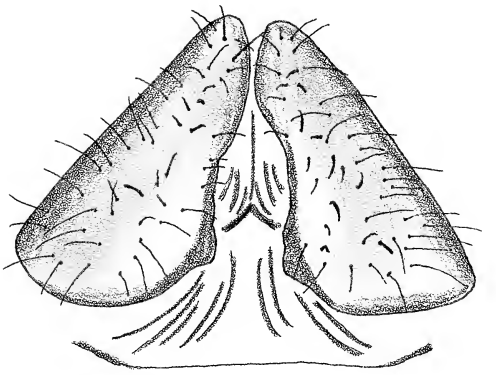

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Figures 10–16.—*Eremobates socal* new species. 10. Dorsal view male propeltidium. 11. Ectal view right male chelicera. 12. Mesal view right male chelicera. 13. Ventral view male right palpus. 14. Ventral view male ctenidia. 15. Ectal view right female chelicera. 16. Ventral view female genital operculum. Scale lines = 1 mm.

tion of the fixed finger of the male chelicera (Fig. 31). Two short, thin to flat ctenidia. It is separated from *E. clarus* by the shape of fixed finger and distinctive female genital operculum.

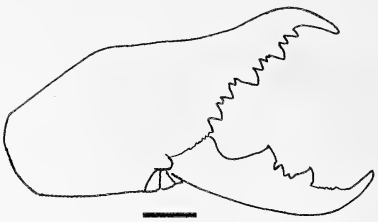
**Description.**—Males: Chelicera, propeltidium and appendages dusky yellow with the following markings: propeltidium blotched dusky purple except for a medial lighter dusky ovoid region (Fig. 47). Some specimens have light violet markings on distal third of leg IV and a chelicera with a dorsal and two lateral dusky purple stripes, abdomen dusky grey.

Chelicera as Muma (1951, fig. 58). FF severely crimped in ectal view (Fig. 31), MF with PT large, AT small, sharp, triangulate, 2 IT, 1st IT separated from PT, cleft under AT, mesal tooth absent, FT graded I, III, II, IV, FT III triangulate and large as FT I, FL/FW equal to or slightly wider, flattened apical plumose bristle occupies 75–80 percent of mesoventral groove, palpal metatarsus with a scopula of 33–80 rounded papillae; 2 short, thin to flat ctenidia (Fig. 42).

*Male measurements(5):* Hanford Site, Benton County, Washington, (WSU). Total length 18.5–25.0, chelicera length 5.00–6.72, chelicera width 2.64–3.04, propeltidium length 2.83–3.33, propeltium width 3.96–4.38, palpus length 15.5–18.0, 1st leg length 13.0–16.0, 4th leg length 22.0–26.0. *Ratios:* A/CP 5.17–6.73, CL/CW 1.84–2.40, FL/FW 0.82–1.07, FW/FFW 1.28–1.55, CW/FFW 4.86–7.08, PL/PW 0.70–0.80.

*Females:* Coloration same as males, chelicera typical of species; FF with PT and MT large, a small AT, two IT between PT and MT, one small IT posterior to the AT; MF with large PT, pointed AT; two small IT, the proximal of which is larger; posterior IT separate from primary tooth; no cleft under AT of MF, MST indistinct or absent. Genital operculum as in fig. 10, p. 19, (Muma 1970) with short, thin arms, medial margin lobed, gently recurved wings ending in a curved posterior margin (Fig. 52). One specimen with 57 rounded papillae on metatarsus of palpus, the rest had none; two tiny hairlike ctenidia were present on one specimen, the rest had none.

*Female allotype:* Total length 19.0, chelicera length 6.4, cheliceral width 3.1, propeltidium length 2.9, propeltidium width 4.16, palpus length 16.0, first leg length 11.0, fourth leg length 22.5. *Ratios:* A/CP 5.32, CL/CW 2.06, PL/PW 7.00, GOL/GOW 0.72. *Female measurements (3)*: Length 19.0–23.0, chelicera length 6.04–7.50, chelicera width 2.29–3.29, propeltidium length 2.58–3.30, propeltidium width 3.96–4.58, palpus length 14.0–17.0, first leg length 11.0–15.0, fourth leg length 18.0–25.0. *Ratios:* A/CP 4.86–5.26, CL/CW 2.28–2.95. PL/PW 0.65–0.73, GOL/GOW 0.50–0.67.



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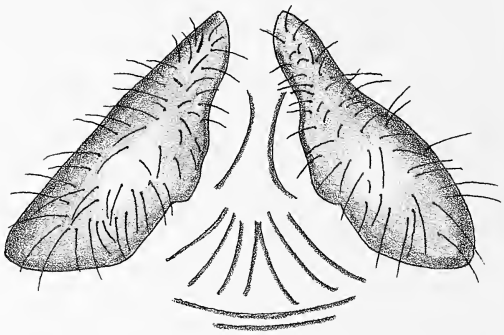

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Figures 17–19.—*Eremobates hodai* Muma. 17. Ectal view female chelicera. 18. Ventral view female genital operculum. 19. Ventral view right male palpus. Scale lines = 1 mm.

**Remarks.**—Muma (1951) described *E. scaber* using a sample population of both males and females from a geographic area extending from Washington state to the deserts of Arizona. He remarked as to the variability of the species and suggested that it might include two or more species. Unfortunately his drawings of the female genital operculum (1951, p. 53, fig. 53) were obviously of another species. After viewing Kraepelin's fe-

male type from Washington Territory, Muma (1970) described *E. scaber* based solely on the type and indicated that males were unknown. In the same publication (Muma 1970) used his 1951 description of *E. scaber* to establish the new species, *E. septentrionis* (Muma 1970).

Muma's (1951) description of *E. gladiolus* listed the male holotype from Maupin, Oregon, the female paratype from Starbucks, Washington, and paratypes from Umatilla, Oregon and Wishrum, Washington, all in the Columbia River Basin. Muma uses only a slight difference in the coloration on leg IV to differentiate the two species. After examination of material from Hanford Test Site in Washington state and Canadian samples from the Okanogan Valley, and the subsequent examination of the types of *E. scaber* and *E. gladiolus*, we have synonymized the two species under *E. scaber* based on the shape of the female genital operculum and the male fixed finger.

The collection sites indicate a range that encompasses the Columbian River Basin, and the Okanogan Valley in northern Washington, USA and the Okanogan Valley, southern British Columbia, Canada which are primarily high desert shrub communities (USEPA 1986).

**Specimens examined.**—Males: UNITED STATES: *Oregon:* Washington County, Maupin (45°10′N, 121°04′W), July 1934, J. M. Pierson (♂, AMNH); Umatilla County, Umatilla (45°55′N, 119°20′W), 24 June 1882, S. Henshaw (♀, AMNH). *Washington:* Benton County, Hanford Nuclear Site (46°32′N, 119°31′W), 23 July–8 August 1999, Rich Zack (8 ♂, 3 ♀, WSU); Whitman County, Wawsweiko Peak (46°32′N, 118°79′W), 27 July 1981, no collector data (♂, WSU). CANADA: *British Columbia:* Osyoos, Haynes Ecological Reserve (49°07′N, 119°40′W), 19 June 1986, S.G. Cannings (2 ♂, Spencer Museum, University of British Columbia); 14 June–3 August 1987 (♂, ♀, ABU); Osyoos, Mount Kobau, 10–33 July 1991, D. Blades & C. Maier (♂, Royal British Columbia Museum, Victoria); Penticton (49°10′N, 119°31′W), 1973, W. D. Charles (♂, ABU); 5 July 1973, M. Redivo (♂ ABU); 27 August 1972, Jose Matias (♂, ABU); Summerland (49°36′N, 119°40′W), 3 July 1928, T. B. Kurta (♀, Royal Ontario Museum, Toronto); August–November 1982, W. D. Charles (♂, ABU); Keremeos (49°12′N, 119°50′W), 6 September 1960, Philip Desjardins (♀, Spencer Museum, University of British Columbia); Oliver (49°11′N, 119°33′W), J. Slack (♀, Spencer Museum, University of British Columbia).

*Eremobates ctenidiellus* Muma 1951
Figs. 32, 38, 48, 55

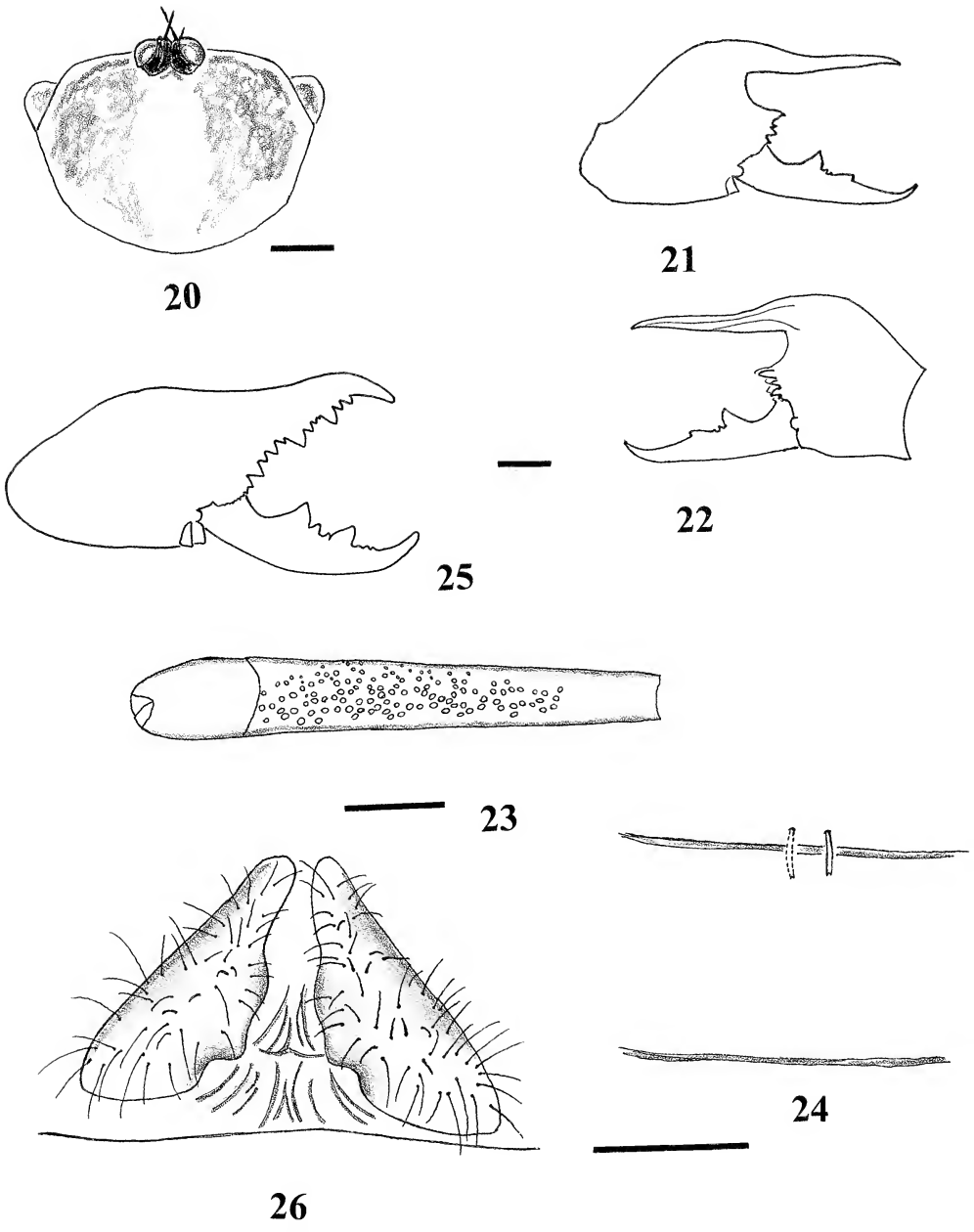
*Eremobates ctenidiellus* Muma 1951: figs. 58–60; Muma 1962:3; Muma 1963:1; Muma 1970:10; Muma & Allred 1971:165; Brookhart 1972:33; Muma 1987:20.

**Type.**—Male holotype and female allotype from 3.2 km west of Glenwood, Sevier County, Utah, US (38°45′N, 111°59′W) 30 June 1940, Gertsch & Hook in AMNH. Muma (1951) lists paratypes in U.S. National Museum, Museum of Comparative Anatomy, USU, Cornell University (Muma 1951) but there are no paratypes at USU (Wilford Hansen pers. comm.).

**Diagnosis.**—Pale species, with 0–2 very thin hairlike ctenidia. Posterior IT of male and female MF in the notch of PT, no cleft under AT. Female genital operculum distinctive with virtually no modification of the interior edge except for a heavily chitinized region which makes it appear as if there is a spot on the medial edge. Fondal notch length equal to width.

**Description.**—Males: Muma's (1951) description is accurate. Appendages pale yellow, propeltidium dusky, violet brown except for a medial pale yellow ovoid region (Fig. 48), abdomen dusky. Chelicera as in fig. 58, p.56, Muma (1951). A thin FF slightly crimped in ectal view, MF with large PT and smaller slightly crumpled AT, no cleft anterior to AT, IT in notch of PT. MST tiny to absent, fondal teeth typical (Fig. 32). Palpus with 50–100 rounded, white papillae on the metatarsal scopula, ctenidia 0–2 thin, hair-like setae (Fig. 38).

*Male holotype:* Total length 22.0, chelicera length 5.6, chelicera width 3.2, propeltidium length 3.0, propeltidium width 4.0, palpus 18.0, 1st leg 15.0, 4th leg 23.0. *Ratios:* A/CP 6.36, CL/CW 3.20, PL/PW 0.75, FL/FW 1.01, FW/FFW 1.25, CW/FFW 5.70. *Male measurements (5):* Total length 17.0–23.0, chelicera length 4.6–6.1, chelicera width 2.2–3.2, propeltidium length 2.4–3.2, propeltidium width 3.3–4.4, palpus length 15.0–18.5, first leg length 13.0–15.0, fourth leg length 17.5–




Figures 20–26.—*Eremobates corpink* new species. 20. Dorsal view male propeltidium. 21. Ectal view male right chelicera. 22. Mesal view male right chelicera. 23. Ventral view male right palpus. 24. Ventral view male ctenidia. 25. Ectal view female chelicera. 26. Ventral view female genital operculum. Scale lines = 1 mm.

25.0. *Ratios:* A/CP 6.15–7.23, CL/CW 1.64–2.34, PL/PW 0.58–0.80, FL/FW 0.80–1.00, FW/FFW 2.67–3.75, CW/FFW 5.50–7.00.

*Females:* Coloration the same as in the males. Chelicera typical of species; MF with posterior IT in notch of PT, no cleft under AT, MST indistinct to absent. Genital operculum as in fig. 60, p. 56 Muma (1951) with short, broad arms, long medial margin with a dark chitinized area midway, very slightly undulate, wings short, posterior margin slightly curved (Fig. 55). No papillae on metatarsus of palpus; two tiny hairlike ctenidia were present on one specimen, the rest had none.

*Female allotype:* total length 19.0, chelicera length 4.6, chelicera width 1.8, propeltidium length 2.5, propeltidium width 3.6, palpus 13.0, first leg length 11.5, fourth leg length 21.5. *Ratios*: A/CP 6.60, GOL/GOW 0.75. *Female measurements (3):* Total length 18.5–21.0, chelicera length 4.6–6.7, chelicera width 2.0–2.4, propeltidium length 2.1–3.0, propeltidium width 3.2–4.2, palpus length 11.5–14.0, first leg length 10.5–13.0, fourth leg length 20.5–22.0. *Ratios:* A/CP 5.05–6.70, CL/CW 2.30–2.79, PL/PW 0.58–0.71, GOL/GOW 0.72–0.82.

**Remarks.**—Measurements were made from specimens collected at various times in Colorado National Monument and adjacent areas. Four males but no females were found by Brookhart in pitfall traps during the summer of 1998. The range of collected specimens indicates an area within the central regions of the Colorado Plateau.

**Specimens examined.**—UNITED STATES: *Colorado:* Mesa County, Colorado National Monument (39°03′N, 108°41′W), 15 July 1962, C.J. McCoy (♂, CU); 21 June 1963, B. Vogel & C.J. McCoy (♂, CU); 29 June 1973, C.J. McCoy (♀, CU); 3 July 1973, C.J. McCoy (♀, CU); Grand Junction (39°03′N, 108°33′W), 26 May–26 August 1998, Jack & Irene Brookhart (4 ♂, DMNS), *Utah:* Grand County, 32 Km west of Glade Park, coordinates unknown, 18 June 1951, no collection data (♂, CU); Emery County, Castle Dale (39°12′N, 111°01′W), 26 June 1951, D.E. Beck (♀, BYU); 7 July 1975, D.M. Allred (♂, BYU); Sanpete County, Manti (39°16′N, 111°38′W), 21 June 1979, Ryan Olson (♀, USU); Sevier County, Richfield, (38°46′N, 112°05′W), 9 July 1963, G. F. Knowlton (♀, BYU).

*Eremobates clarus* Muma 1989
Figs. 33, 36, 45, 54

*Eremobates clarus* Muma 1989:10.

**Type.**—Male holotype at 2194 meters in pitfall trap, Saratoga Stratton Experimental Watershed, Carbon County, Wyoming, US (41°27′N, 106°48′W), 17–21 July 1973, collected by John Schmid, AMNH. One male paratype from same trap (AMNH).

**Diagnosis.**—Distinguished from closely related *E. scaber* by less crimped, more smoothly curved FF in ectal view, and the cleft under the AT of the MF. Female operculum has broader anterior arms and less undulation of the medial margin of the genital operculum. It is distinguished from *E. ascopulatus* by its pale coloration, slightly different female genital operculum, and shape of ctenidia.

**Description.**—Males*:* Muma adequately described the male in 1989. Overall coloration very pale yellow, propeltidium dusky violet brown similar to *E. scaber* but with a larger median pale ovoid region, abdomen dusky, palpus and all legs pale yellow. Some specimens are duskier on propeltidium and appendages.

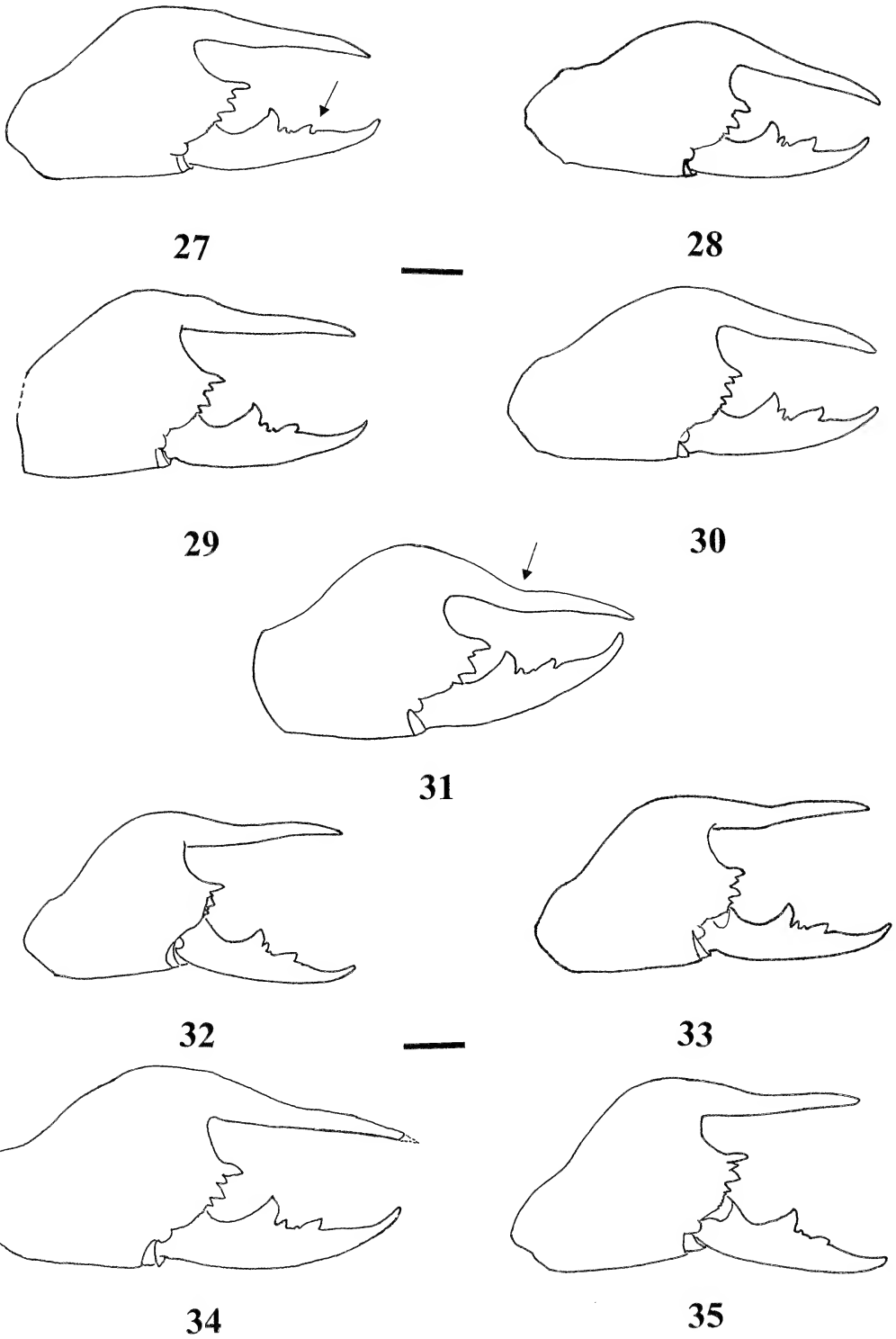
Thick, male FF gently curved to only slightly upturned in ectal view, no teeth, MF with posterior IT separate from PT, AT with anterior cleft, MST absent, FT graded I, III, II, IV, Fondal notch equal to or slightly wider (Fig. 33). Palpal papillae 33—80 +, two tiny, peg-like ctenidia (Fig. 36).

*Male holotype:* Total length 19.0, chelicera length 4.7, chelicera width 2.3, propeltidium length 2.3, propeltidium width 3.4, palpus length 16.0, first leg length 12.0, fourth leg length 20.0. *Ratios*: A/CP 6.86, PL/PW 0.76, CL/CW 2.04, FL/FW 0.72. *Male measurements(5):* Length 18.0–22.0, chelicera length 4.6–6.6, chelicera width 2.2–3.2, propeltidium length 2.2–2.6, propeltidium width 3.4–3.6, palpus length 13.5–17.0, first leg length 11.0–12.5, fourth leg length 17.0–21.0. *Ratios:* A/CP 5.32–6.86, CL/CW 1.86–2.19, PL/PW 0.63–0.72, FL/FW 0.80–1.20, FW/FFW 2.80–3.75, CW/FFW 4.40–6.40.

*Females:* Coloration as in males, chelicera typical of group. Posterior IT of MF separate. Cleft under AT, MST tiny. Genital operculum with short, broad arms, medial margin undulate forming two small lobes, arms long, gently curved, posterior margin rounded (Fig. 54).

Female measurements(6)*:* Length 18.0–24.0, chelicera length 4.8–6.4, chelicera width 2.20–2.65, propeltidium length 1.6–2.6, propeltidium width 3.0–3.6, palpus length 13.0–15.5, first leg length 9.5–11.2, fourth leg length 16.0–21.0. *Ratios:* A/CP 4.92–6.97 CL/CW 2.04–2.50, PL/PW 0.50–0.72, GOL/GOW 0.46–0.56.

**Remarks.**—*Eremobates clarus* was collected by Brookhart during the summer of 1998 from pitfall traps placed in both Piñon pine-Juniper and greasewood (*Sarcobartus* sp.) habitats in northwest Colorado near Dinosaur National Monument. It appears to occupy the area




Figures 27–35.—Ectal view male right chelicerae (arrow shows cleft under anterior tooth). 27. *E. zinni*. 28. *E. similis*. 29. *E. mormonus*. 30. *E. actenidia*. 31. *E. scaber* (arrow showing "crimp" in male fixed finger). 32. *E. ctenidiellus*. 33. *E. clarus*. 34. *E. hodai*. 35. *E. ascopulatus*. Scale lines = 1 mm.

encompassed by the Laramie Plateau. The female is described for the first time.

**Specimens examined.**—UNITED STATES: *Colorado:* Moffat County, Castle Park, Dinosaur National Monument (40°28′N, 108°53′W), 18–30 June 1948, Hugo Rodeck (4 ♂, CU); 4 July 1949, Hugo Rodeck (♂, ♀, CU); 3.2 Km W of Craig (40°30′N, 107°32′W), 26 May–16 June 1971, Jack & Irene Brookhart (2 ♂'s, ♀, CU); 35.4 Km W of Craig, 18 June 1993, no collector (♀, CU); 19.3 Km W of Craig, 1 May–26 July 1998, Jack & Irene Brookhart (3 ♂, DMNS). *Wyoming:* Carbon County, Saratoga Stratton Experimental Station (41°27′N, 106°48′W), Jon Schmid, (♂, DMNS).

*Eremobates hodai* Muma 1989
Figs. 17–19, 34, 40, 46

*Eremobates hodai* Muma 1989:13, fig. 14.

**Type.**—*Eremobates hodai* male holotype labeled College of Idaho with no other information. Deposited in FSCA.

**Diagnosis.**—Related to *E. scaber* and *E. clarus* from which it differs in coloration, shape of fondal notch, and female genital opercula. Although the holotype lacks palpal papillae and ctenidia other male specimens have papillae and ctenidia.

**Description.**—Males*:* Pale yellow coloration, palpus, legs pale, anterior region of propeltidium pale violet, eye tubercle dark. Chelicera pale with no stripes, typical dentition, FF crimped in ectal view, MF with posterior IT separate from PT, no cleft under AT (Fig. 34). Two short, pointed ctenidia (Fig. 40), 75–106 palpal papillae (Fig. 19).

*Male holotype:* Total length 21.0, chelicera length 6.5, chelicera width 3.3, propeltidium length 3.5, propeltidium width 4.0, palpus length 20.0, first leg length 17.5, fourth leg length 25.0. *Ratios:* A/CP 6.35, CL/CW 1.70, PL/PW 0.88, CL/CW 2.20, FL/FW 0.88, FW/FFW 1.14, CW/FFW 4.00. *Male measurements (3):* Total length 17.0–23.0, chelicera length 6.25–6.46, chelicera width 2.17–3.00, propeltidium length 2.71–3.42, propeltidium width 3.54–4.67, palpus length 15.0–19.0, first leg length 11.0–15.5, fourth leg length 19.0–22.0. *Ratios:* A/CP 5.07–5.77, CL/CW 2.15–2.98, PL/PW 0.73–0.76, CL/CW 2.15–2.98, FL/FW 0.95–1.00, FW/FFW 1.33–1.42, CW/FFW 4.73–5.17.

*Females:* Coloration as in males. Chelicera typical, posterior IT separate from PT, no cleft under AT (Fig. 17). Genital opercula similar to *E. scaber* with long, broad arms, medial margin slightly curved inward, wings offset, long, posterior margin short ending in a point (Fig.18). *Female measurements (3):* Total length 18.0–22.0, chelicera length 4.71–7.29, chelicera width 2.58–3.33, propeltidium length 2.83–3.33, propeltidium width 4.17–5.00, palpus length 13.0–15.0, first leg length 11.0–13.0, fourth leg length 18.0–21.0. *Ratios*: A/CP 4.61–5.83, CL/CW 1.66–2.00, PL/PW 0.66–0.70, GOL/GOW 0.82–0.86.

**Remarks.**—*Eremobates hodai* was found in the Snake River Plain region of the Columbia River Plateau (USEPA 1986). Allred & Muma (1971) identified *E. septentrionis*, now *E. ascopulatus* and *E. ctenidiellus* from this region but were in error. Although this species may later be synonymized with *E. clarus* or *E. scaber*, its small A/CP and its pale lemon coloration leads us to separate it at this time.

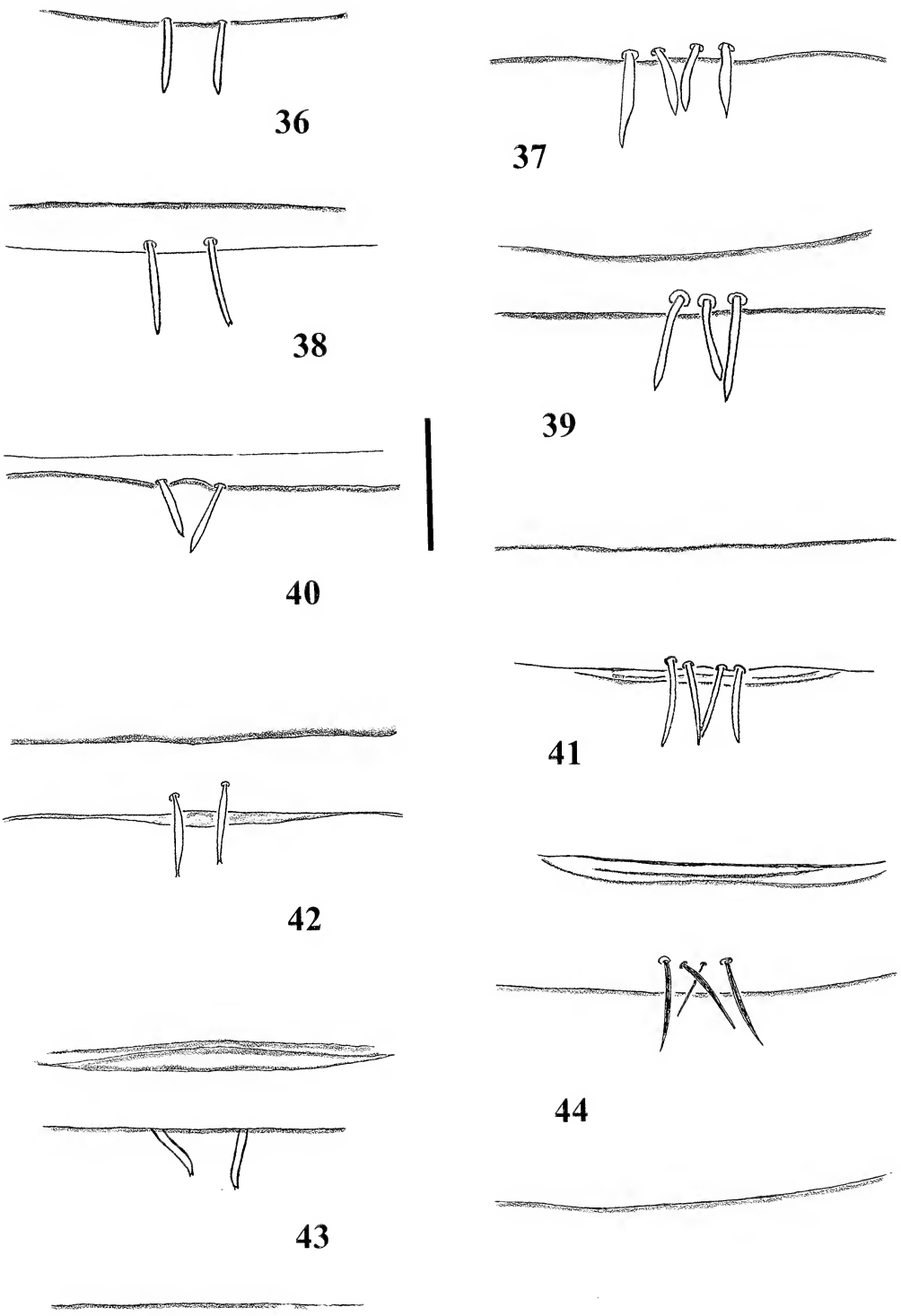
**Specimens examined.**—UNITED STATES: *Idaho:* Ada County, Eagle (43°41′N, 116°21′W), August 1987, W.H. & Mary Clark (2 ♀, ID); Butte County, 30 Km E of Arco, 6 June 1987, W.H. & Mary Clark (♂, ID); 41.8 Km SE of Howe, W.H. & Mary Clark (♀, ID); 35.4 Km SE of Howe, 2–16 July 1987, P. Blom, W.H. Clark (♂, ID). *Oregon:* Baker County, Sumpter (label says Idaho) (45°05′N, 113°44′W), 26 July 1995, W.H. & Mary Clark (♂, ♀, ID).

*Eremobates ascopulatus* Muma 1951
Figs. 35, 43, 49, 53

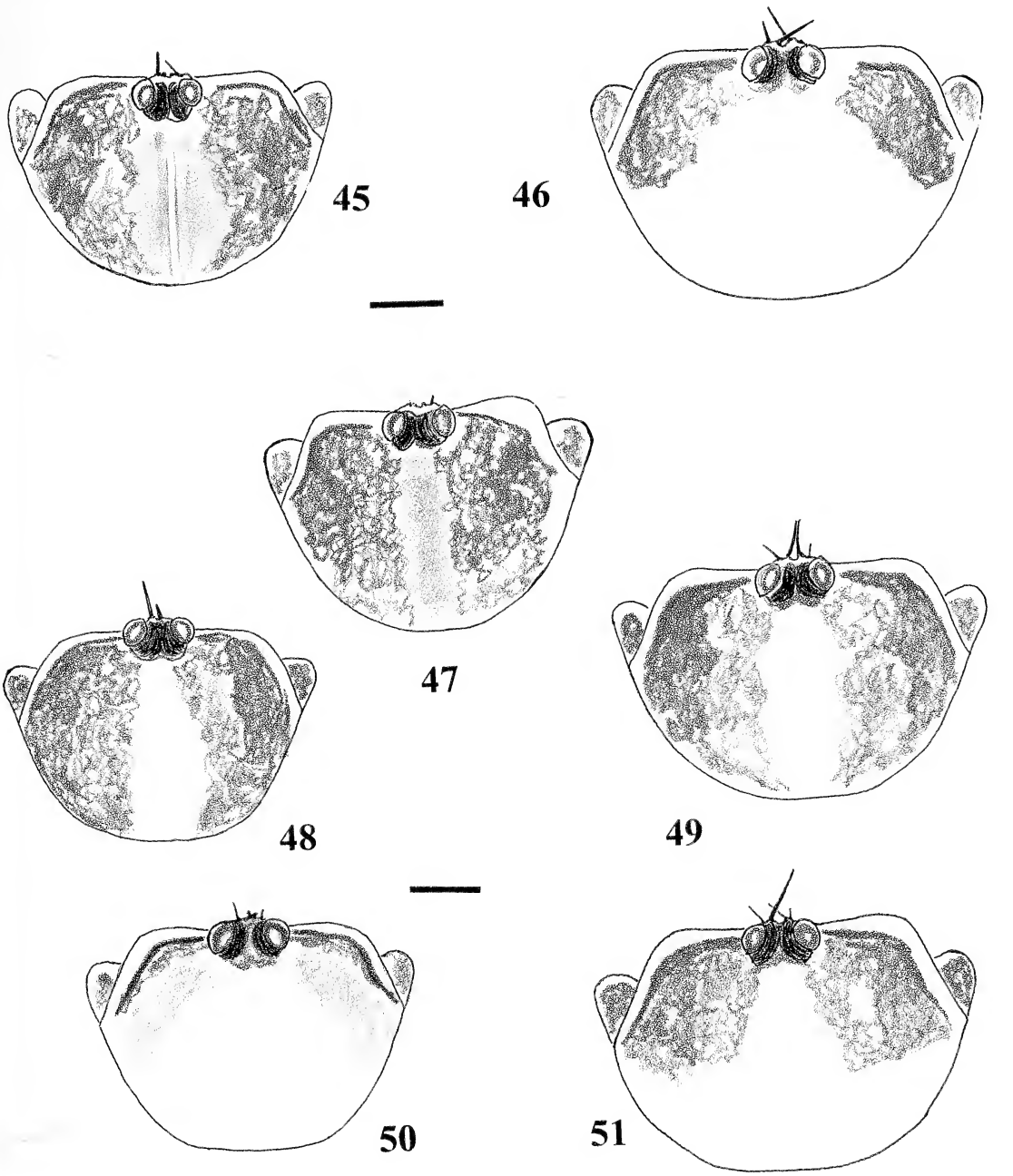
*Eremobates ascopulatus* Muma 1951:60, fig. 19.
*Eremobates scaber* (Kraepelin) *sensu* Muma 1951: 52–55, figs. 44–53 (not *E. scaber* Kraepelin).
*Eremobates septentrionis* Muma 1970:12–14; Muma & Allred 1971:164; Brookhart 1972:33. NEW SYNONYMY.
*Eremobates flavus* Muma 1989:11–12, figs. 7–9. NEW SYNONYMY.
*Eremobates consors* Muma 1989:11, figs. 5–6. NEW SYNONYMY.

**Type.**—Male holotype of *E. septentrionis* from Richfield, Utah, Sevier County, 20 June 1930, W.J. Gertsch (AMNH).

*Eremobates flavus*: Male holotype collected in Reno, Washoe County, Nevada by W.F. Hendrick, 7 July 1972; female allotype collected in Jungo, Humboldt County, Nevada by L.L. Stitt (holotype and allotype in FSCA).




Figures 36–44.—Ventral view of male ctenidia. 36. *E. clarus*. 37. *E. mormonus*. 38. *E. ctenidiellus*. 39. *E. zinni*. 40. *E. hodai*. 41. *E. similes*. 42. *E. scaber*. 43. *E. ascopulatus*. 44. Female *E. similis*. Scale lines = 1 mm.




Figures 45–51.—Dorsal view male propeltidia. 45. *E. clarus*. 46. *E. hodai*. 47. *E. scaber*. 48. *E. ctenidiellus*. 49. *E. ascopulatus*. 50. *E. zinni*. 51. *E. mormonus*. Scale lines = 1 mm.

*Eremobates consors*: Female holotype from Minden, Douglas County, Nevada collected by D.A. Ball (Code #83H30-2 FSCA).

**Diagnosis.**—*Eremobates ascopulatus* appears to be related to *E. clarus*. It is distinguished by the shape of male chelicera, coloration of palpus and shape of female genital opercula.

**Description.**—Male: Overall coloration dusky, straw yellow, chelicera with two dusky purple patches dorsally and one laterally, propeltidium tinged dusky purple anteriorly and laterally creating a broad, dusky yellow, ovoid

area (Fig. 49), abdomen grey to dark grey, palpal tarsus and metatarsus darker than the other appendages. Occasionally specimens have legs that are dusky at the tibia-femur joint. Some northern California specimens are darker, particularly the propeltidium and palpus.

Male FF only slightly upturned in ectal view, posterior IT separate from PT, small, triangulate AT without a cleft, fondal notch L/W highly variable, MST medium (Fig. 35), 60–80 + palpal papillae on most specimens, two short peg-like ctenidia (Fig. 43).

*Male holotype:* Total length 21.0, chelicera length 5.76, chelicera width 2.73, propeltidium length 3.1, propeltidium width 3.8, palpus length 18.0, first leg length 15.0, fourth leg length 23.5. *Ratios:* A/CP 6.60, CL/CW 2.10, PL/PW 0.81, FL/FW 1.20, FW/FFW 1.38, CW/FFW 6.20. *Male measurements (5):* Total length 19.5–23.0, chelicera length 5.25–6.13, chelicera width 2.45–2.98, propeltidium length 2.80–2.98, propeltidium width 3.85–4.20, palpus length 16.0–19.5, first leg length 14.5–16.5, fourth leg length 20.0–23.5. *Ratios*: A/CP 6.27–6.62, CL/CW 1.82–2.19, PL/PW 0.68–0.73, FL/FW 0.74–1.22, FW/FFW 1.25–1.54, CW/FFW 4.86–7.08.

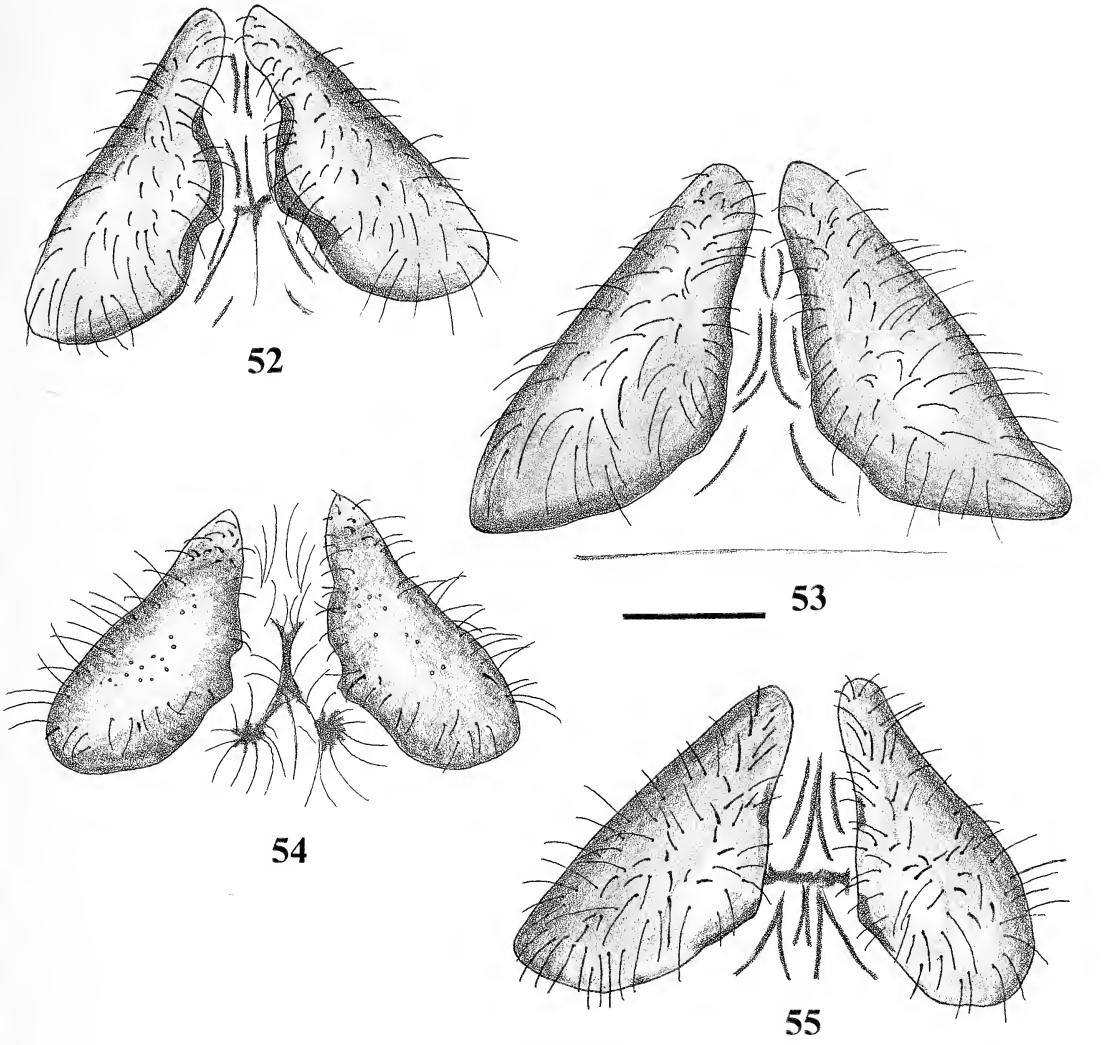
*Females:* Coloration as in males. Chelicera typical of scaber group. MF with posterior IT in the notch of PT, no cleft anterior to AT. Genital opercula similar to *E. ctenidiellus* and *E. geniculatus* with long broad arms, slightly undulate medial margin, short wings, curved posterior margin (Fig. 53). *Female measurements (4):* Total length 18.5–27.0, chelicera length 5.0–7.6, chelicera width 2.4–3.2, propeltidium length 2.4–3.2, propeltidium width 3.8–5.4, palpus 15.0–19.0, first leg length 10.0–14.5, fourth leg length 20.0–25.0. *Ratios:* A/CP 4.96–5.90, CL/CW 2.08–2.73, PL/PW 0.55–0.74, GOL/GOW 0.42–0.80.

**Remarks.**—Muma (1951) misidentified *E. septentrionis* as *E. scaber* but after examining the holotype of the latter in Europe erected *E. septentrionis* using his 1951 description of *E. scaber* (1970). He deviated from the original description in describing the palpal color as dusky purple. We here synonymize *E. septentrionis* with *E. ascopulatus* based on examination of both types which differ in only the absence of palpal papillae in *E. ascopulatus*. In this study we have found that in large samples of papillate species there is an occasional specimen without papillae. Our ongoing research seems to indicate that papillae may arise sequentially after the penultimate molt. *Eremobates ascopulatus* is known from only two male specimens both of which were found in the same geographic area as *E. septentrionis*. Because the description of *E. septentrionis* was based on specimens from many disparate parts of the western United States we have redescribed *E. ascopulatus* based on the holotype and reinforced by sample specimens.

Muma (1989) remarked as to the similarity between *E. septentrionis* and *E. flavus* and suggested that they may be the same species. We have found this to be the case. Muma's (1989) holotype of *E. flavus* from Reno, Nevada had longer, thinner ctenidia but other specimens from this area and nearby northeastern California had ctenidia and female genital opercula as in *E. septentrionis*. Some of the northern California specimens were darker in overall color suggesting perhaps a sibling species but more specimens are needed for examination. *Eremobates consors* is known from only one female and erected based on the shape of the female genital operculum. Examination of the holotype indicates that the operculum was desiccated and is in reality *E. ascopulatus*.

*Eremobates ascopulatus* has a range that encompasses the Bonneville Basin and Lohantan Basin (see Trimble 1989) of northern Utah, Nevada, and northeastern California. It was also found at the Nevada Test Site (Muma 1963) where it is sympatric with *E. zinni*. Hall (1946) remarked as to the "intimate ecological connections" between the Lahontan basin and the Mojave Desert region of southern Nevada. These areas have the typical Great Basin desert shrub habitat. It appears to be related to *E. clarus* and *E. ctenidiellus*.

**Specimens examined.**—UNITED STATES: *California:* Placer County, Lake Tahoe (39°10′N, 120°08′W), no date, Hubbard & Swartz, (♂, FSCA); 11 July 1952, W.J. Gertsch (♀, AMNH); Plumas County, Lake Almanor (40°13′N, 121°10′W), 7 July 1952, W. J. Gertsch (♂, AMNH); 6.4 Km W of Quincy (39°56′N, 120°56′W), 21 June 1949, J. W. MacSwain (3 ♂ AMNH); Shasta County, Castella (41°08′N, 122°19′W), 26 July 1935, W. J. Gertsch (♀, AMNH). *Nevada:* Elko County, 14.5 Km S of Contact, M.H. Muma (♂, FSCA); Pershing County, Lovelock (40°10′N,




Figures 52–55.—Ventral view female genital opercula. 52. *E. scaber*. 53. *E. ascopulatus*. 54. *E. clarus*. 55. *E. ctenidiellus*. Scale line = 1 mm.

118°28′W), 22 June 1972, A.G. Rose (♀, FSCA); Washoe County, Reno (39°31′N, 119°48′W), 15 August 1989, P. C. Martenelli (2 ♂, ♀, FSCA). *Utah:* Box Elder County, Lucin (41°20′N, 113°54′W), 19 June 1952, D.E. Beck (2 ♂, BYU); Cache County, Logan (41°44′N, 111°50′W), 4 July 1949, Steve Dewey (♂, USU); 10 July 1995, D. Rasmussen (♂, USU); Davis County, Hill Air Force Base (The county designation is probably incorrect as Hill Air Force Base Recreation Area is located in Weber County, not Davis County. See coordinates below under Weber County.), 17 July 1991, Mike Peterson (♂, BYU); Salt Lake County, Sandy (40°35′N, 111°53′W), 24 June 1985, Teresa Tipton (♂, USU); Utah County, Alpine (40°27′N, 111°46′W), 24 June 1997, A.L. Huillet (♂, BYU); Environs, no coordinates, 14 June 1972, Troy Cooper (♀, USU); Orem (40°17′N, 111°41′W), 20 June 1988, R. Williams (♀, BYU); 7 July 1993, Lisa Trotter (♂, BYU); Provo (40°14′N, 111°39′W), 1 September 1993, D.O. White (♀, BYU); Santaquin (39°58′N, 111°47′W), 18 July 1987, J. Jarvis (♀, USU); Spanish Fork (40°06′N, 111°39′W), 8 July 1979, D. C. Holt (♀, USU); Tooele County (says Uintah County on label), Vernon (40°05′N, 112°25′W), 7 August 1964, K. Bendixs (♀, USU); Weber County, Hill Air Force Base (41°13′N, 111°50′W), 27 July 1995, Larry Sanders (♂, BYU).

***Eremobates icenoglei*** new species
Figs. 4–9

**Type.**—Male holotype collected by W. Icenogle in wet pit-fall trap, 29 August 1996, Winchester (33°42′N, 117°05′W), Riverside County, California; female allotype collected by W. Icenogle 22 Aug 1966 in wet pit-fall trap, Riverside County, California, 5 male paratypes, 5 female paratypes collected by W. Icenogle, Winchester, California, Riverside County in wet pit-fall traps 29 August 1967–23 August 1996. All types deposited in DMNS.

**Etymology.**—Named for the collector Wendell Icenogle of Winchester, California.

**Diagnosis.**—*Eremobates icenoglei* new species appears most closely related to *E. zinni* but is separated from it and others of the scaber group by absence of AT on male MF, a fond that is noticeably longer than wide, and a thickened FF. The female genital operculum is distinctive (Fig. 9).

**Description.**—Males*:* Coloration overall dark to dusky yellow, abdominal tergites dusky, appendages dusky yellow with palpal metatarsus and the tibia-femora joint area dusky violet-brown, propeltidium dusky purple on anterior edge and top lateral one third (Fig 4).

Fixed finger of chelicera with little or no crimping, fondal notch longer than wide; width of FF 80% the width of FN; MF with large primary tooth, and a ridge that is slightly elevated anteriorly instead of intermediate and anterior teeth, MST intermediate in size (Fig. 5–6). Four stiletto shaped ctenidia on first post-spiracular sternite extending approximately half the length of the sternite (Fig. 7); no palpal papillae.

*Male holotype:* Total length 19.0, chelicera length 4.8, chelicera width 2.2, propeltidium length 2.6, propeltidium width 3.5, palpus length 16.0, first leg length 16.0, fourth leg length 23.0. *Ratios*: A/CP 6.82, CL/CW 2.20, FL/FW 1.40, WFF/FW 1.20, CW/WFF 4.23. *Male paratypes (5):* Total length 18.0–24.0, chelicera length 5.50–6.92, chelicera width 4.4–6.4, propeltidium length 2.32–3.20, propeltidium width 3.2–4.0, palpus length 14.0–17.0, first leg length 10.0–14.0, fourth leg length 17.0–24.0. *Ratios:* A/CP 5.52–6.80, CL/CW 1.73–2.20, FL/FW 1.17–1.44, FW/FFW 2.29–3.75, CW/WFF 4.23–5.75.

*Female:* Coloration the same as male. Chelicera typical of species; MF with posterior IT separate from PT, MST indistinct to absent (Fig. 8), no papillae on metatarsus of palpus; 2–3 tiny hairlike ctenidia were present on two specimens, the rest had none. Genital operculum with longer, broad arms, a long, slightly recurved medial surface ending in a point, wing short to absent, and posterior edge truncated (Fig. 9). *Female (allotype):* Total length 19.0, chelicera length 6.2, chelicera width 2.8, propeltidium length 2.0, propeltidium width 3.6, palpus length 12.0, first leg length 9.0, fourth leg length 17.5. *Ratios*: A/CP 4.70, CL/CW 2.20, PL/PW 0.55, GOL/GOW 0.82. *Female paratypes (5):* Total length 17.0–26.0, chelicera length 4.8–7.6, chelicera width 1.8–3.4, propeltidium length 2.0–3.0, propeltidium width 3.5–5.0, palpus length 12.0–16.0, first leg length 9.0–13.0, fourth leg length 16.0–22.0. *Ratios:* A/CP 4.70–5.66. CL/CW 2.20–2.67, PL/PW 0.48–0.63, GOL/GOW 0.74–0.82.

**Remarks.**—*Eremobates icenoglei* appears to be restricted to the Coastal Chaparral habitat. It was found by Wendell Icenogle in buildings and in pitfall traps.

**Specimens examined.**—UNITED STATES: *California:* Riverside County, Winchester (33°42′N, 117°05′W), 29 August 1967 (♂, 3 ♀), 16 September 1967 (2 ♀); 24 September 1968 (♀), 11 August 1973 (3 ♂), 3 September 1973 (3 ♀), 4 September 1973 (♀), 8 August 1981 (4 ♂), 17 August 1987 (3 ♂), 16 August 1988 (2 ♂), 1 August 1996 (2 ♂), 23 August 1996 (♂). All collected by Wendell Icenogle. Types and paratypes in DMNH.

*Eremobates mormonus* (Roewer 1934)
Figs. 29, 37, 51, 57

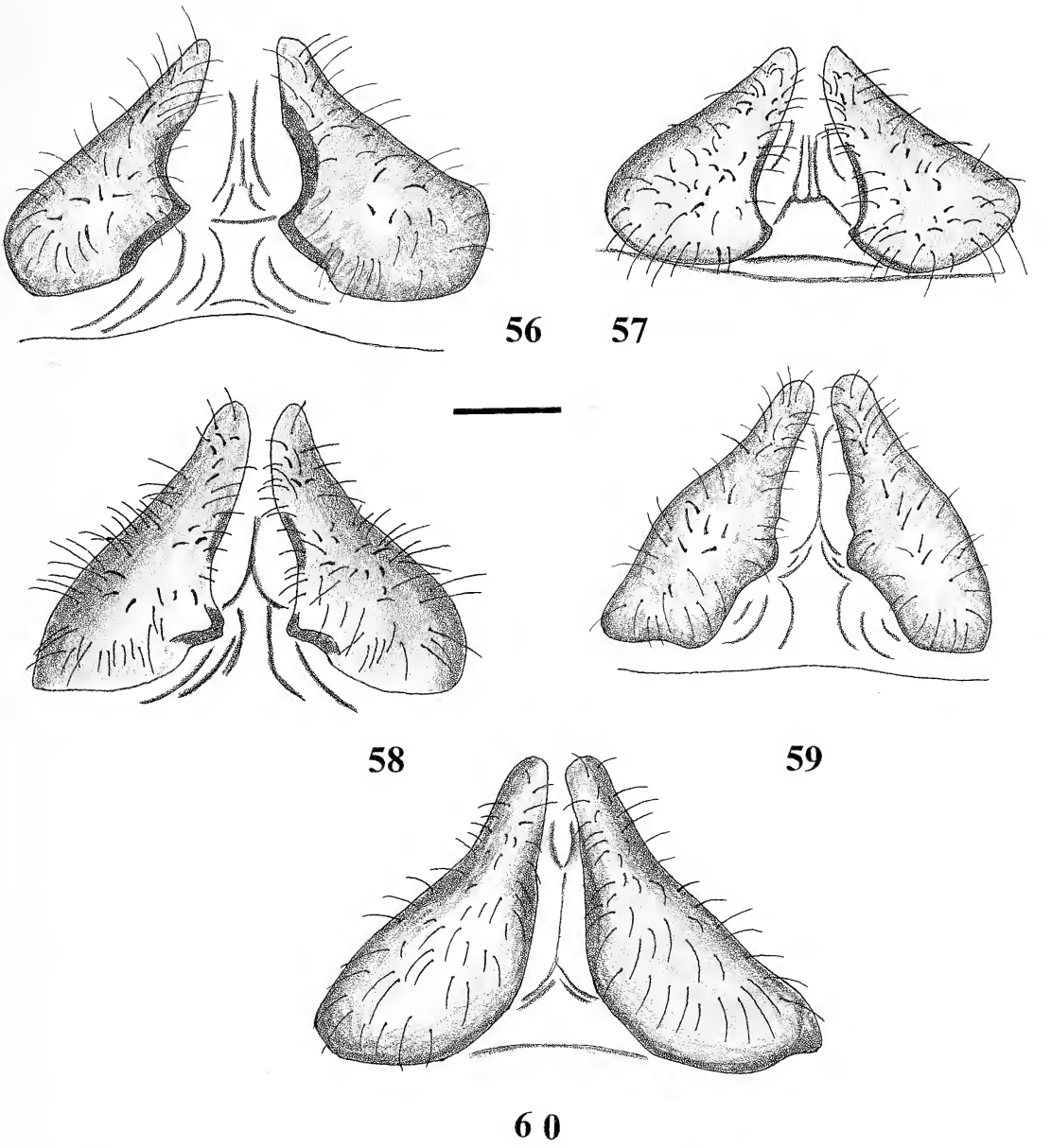
*Eremoperna mormona* Roewer 1934:561, figs. 323e, 324f.

*Eremoperna mormonus* (Roewer); Muma 1962:1; Muma 1970:12, fig. 9; Brookhart 1972:32.

*Eremobates geniculatus* (Simon) *sensu* Muma 1951:55–57 (misidentification).

*Eremobates mimbrenus* Muma 1989:12–13, figs. 10–13. NEW SYNONYMY.

**Type.**—Female holotype of *Eremoperna mormona* from Utah, SMF/RII/3446. No specific locality or collector indicated. Male holotype of *E. mimbrenus* from Signal Peak (32°55′N, 108°10′W), Grant County, New Mexico, 17 June 1976 and female allotype




Figures 56–60.—Ventral view female genital opercula. 56. *E. similis*. 57. *E. mormonus*. 58. *E. zinni*. 59. *E. actenidia*. 60. *E. legalis*. Scale lines = 1 mm.

from same locality collected on 1 July 1976. Both collected by Martin Muma (FSCA).

**Diagnosis.**—This species appears closely related to *E. similis* Muma but can be distinguished from it by its darker color, shape of fondal notch, presence of papillae, and thickness and length of ctenidia.

**Description.**—*Males:* Coloration dusky straw yellow over all, propeltidium dusky purple anteriorly and on the lateral one third (Fig. 51), tergites with broad violet brown stripe, abdomen grey, palpal tarsus and metatarsus dusky amber, legs dusky amber on femur-tibia joint. FF regularly curved; MF with large PT and AT, no cleft under AT, posterior IT in the notch of PT, MST tiny to absent. Fondal notch wider than long (Fig. 29); ctendia 4 flat, sword like, extending slightly more than half the length of succeeding sternite (Fig. 37); 80+ papillae on palpal scopula. Apical plumose

bristle covers most of mesal groove. *Male measurements (5):* Total length 15.0–23.0, palpus length 10.0–22.0, first leg length 9.0–14.5, fourth leg length 14.5–23.0, chelicera length 3.5–5.4, chelicera width 1.6–2.6, propeltidium length 1.6–2.8, propeltidium width 2.00–3.85. *Ratios:* A/CP 6.08–7.59, CL/CW 1.94–2.20, PL/PW 0.70–0.80, FL/FW 0.50–0.67, FW/FFW 1.25–1.88, CW/FFW 4.60–6.20.

*Females:* Coloration same as males. Chelicera typical of species; MF with posterior IT in the notch of PT, no cleft under AT. MST indistinct to absent. Genital operculum similar to *E. zinni* and *E. socal*, new species as in fig. 68, pg. 59, Muma 1951 with short arms, medial surface gently curved ending in a point as in *E. zinni* and *E. similis*, short curved wing (Fig. 57). No papillae on metatarsus of palpus; seven tiny hairlike ctenidia were present on one specimen.

*Female allotype:* Total length 19.0, chelicera length 5.1, chelicera width 2.2, propeltidium length 2.3, propeltidium width 3.9, palpus length 12.5, first leg length 11.0, fourth leg length 18.5. *Ratios:* A/CP 5.75, CL/CW 2.31, PL/PW 5.90, GOL/GOW 0.54. *Female measurements (3)*: Total length 18.5–21.0, chelicera length 4.40–5.02, chelicera width 2.0–2.1, propeltidium length 2.1–3.0, propeltidium width 3.4–3.6, palpus length 11.5–12.0, first leg length 10.5–12.0, fourth leg length 18.0–22.0. *Ratios:* A/CP 5.34–6.16, CL/CW 2.20–2.40, PL/PW 0.58–0.94, GOL/GOW 0.54–0.63.

**Remarks.**—This species was erroneously described as *E. geniculatus* by Muma 1951, but after examining the holotype in Paris he identified it as Roewer's species from Utah. Muma (pers. comm.) stated that the "type" of *E. mormonus* in the collection of MNHN is not Koch's type but may be a lectotype set up by Roewer and therefore invalid. No other locality data were given but it must have been somewhere in southwest Utah based on the presence of other species in that area. We found *E. mormonus* in northern Arizona around the Grand Canyon, SW Colorado and western New Mexico on mesas with sage, piñon pine-juniper and alpine meadows. The Arizona specimens are darker in overall coloration. We here synonymize *E. mimbrenus* with *E. mormonus*. *Eremobates mimbrenus* was described by Muma (1989), and the description that Muma gave is correct except that in his drawing of the right male chelicera, the IT is shown on the PT yet on the type specimen itself, the IT is separate (Muma 1989, fig. 12). In the same vial is a male and female, collected by Muma that appear to be *E. mormonus* as well as two other vials from the area with two males and a female which also key out to *E. mormonus*. Muma's (1989) description of the female allotype of *E. mimbrenous* was based on a female with three intermediate teeth on the movable finger collected in a pitfall trap in SW New Mexico. A female in the same vial does not have this character and could be recognized as *E. mormonus* based on genital opercula and chelicera structure. The male in the same vial is also recognized as *E. mormonus*. Until more specimens are collected from this area we have synonymized *E. mormonus* and *E. membrenus*.

**Specimens examined.**—UNITED STATES: *Arizona:* Coconino County, North rim of Grand Canyon (36°12′N, 112°03′W), 13 July 1934, Rockefeller, (2 ♀, AMNH); 18 July 1934, Lutz (♂, ♀, AMNH); 13 June 1934, Wilton Ivie (♂, AMNH); Flagstaff (35°11′N, 111°39′W), 22 July 1949, Billy Hughes (♀, AMNH); Kaibob Forest (35°50′N, 112°05′W), 14 June 1934, Ivie & Rasmussen (♂, AMNH). *Colorado:* Montezuma County, Chimney Rock (37°04′N, 108°43′W), 31 July 1973, B. Vogel (2 ♂'s, CU); McFee Reservoir (misspelling of McPhee Reservoir) (37°34′N, 108°34′W), 28 August 1997, B. Jacobi (2 ♂, 2 ♀, CSU); Miller Reservoir (37°37′N, 108°27′W), 28 August 1997, no collector (♂, CSU); Mesa Verde National Monument (37°14′N, 108°28′W), 23 July 1941, no collector (2 ♂, ♀, CU). *New Mexico:* Grant County, Signal Peak, Gila National Forest (32°55′N, 108°10′W), 6 July 1976, 1 July 1976), Martin Muma (2 ♂, ♀, FSCA).

*Eremobates similis* Muma 1951
Figs. 28, 41, 56

*Eremobates similis* Muma 1951:figs. 70–71; Muma 1962:4; Muma 1970:14; Muma 1989:9.

**Type.**—Male holotype, Elk Ridge, Utah County, Utah (40°00′N, 111°40′W), 13 June 1936, Douglas Henriques, originally deposited at University of Utah but now at AMNH.

**Diagnosis.**—Lighter coloration with a more violet tinge than the closely related *E. mor-*

*monus* with 4–6 short, thin, needle like ctenidia extending less than half the length of succeeding sternite, no palpal papillae.

**Description.**—*Males:* Appendages and propeltidium straw yellow with violet brown markings. Propeltidium lightly blotched violet brown on anterior and lateral margins, palpus and legs violet brown on femur, tibia, metatarsus, tarsus, abdominal tergites yellow grey. FF regularly curved in ectal view with no teeth; MF with posterior IT situated in the notch; AT triangulate with no cleft; MST tiny to absent. Fond significantly wider than long (Fig. 28); 4–6 thin, needle like ctenidia on first post spiracular sternite extending less than half the length of the sternite (Fig. 41). No papillae on palpal scopula. Both male and female descriptions are made from specimens collected in wet pit fall traps in Costillo County, Colorado in the summer of 1997 by J.O. and I.P. Brookhart. They were the most common solifugid found in the San Luis Valley of Colorado. They were referred to as *E. mormonus* by Brookhart (1972).

*Male holotype:* Total length 22.0, chelicera length 5.2, chelicera width 2.6, propeltidium length 2.5, propeltidium width 3.9, palpus length 17.0, first leg length 14.0, fourth leg length 22.0. *Ratios*: A/CP 6.88, CL/CW 2.00, PL/PW 0.64, FL/FW 0.50, FW/FFW 1.66. *Male measurements (6) (from San Luis Valley, Colorado):* Total length 15.5–17.0, chelicera length 4.2–4.8, chelicera width 1.8–2.0, propeltidium length 2.0–2.2, propeltidium width 2.8–3.2, palpus 12.0–18.0, first leg length 11.0–16.5, fourth leg length 17.0–20.0. *Ratios:* A/CP 6.52–7.69, CL/CW 2.22–2.44, PL/PW 0.63–0.71, FL/FW 0.62–0.71, FW/FFW 3.50–4.33, CW/FFW 5.50—6.50.

*Females:* Coloration as in males, chelicera typical of species; MF with posterior IT in the notch of PT; MST indistinct to absent. Genital operculum with short, thin arms, interior lateral surface curved ending in a point as in *E. zinni* and *E. mormonus*, long recurved wings, rounded posterior margin (Fig. 56). No papillae on metatarsus of palpus; 2–5 tiny hairlike ctenidia were present on most specimens (Fig. 44).

*Female measurements (6):* Total length 16.5–22.0, chelicera length 4.20–5.52, chelicera width 1.8–2.4, propeltidium length 2.0–2.6, propeltidium width 3.0–4.0, palpus length 10.0–15.0, first leg length 8.0–11.5, fourth leg length 14.0–21.0. *Ratios*: A/CP 5.30–5.76, CL/CW 2.33–2.88, PL/PW 0.62–0.81, GOL/GOW 0.58–0.71.

**Remarks.**—*Eremobates similis* was described from a specimen with a locality label from Salt Lake City, Utah. Although the type locality for *E. similis* is listed as Salt Lake City, Utah we have collected this species only in an area that can be roughly called the northern Rio Grande Valley at three sites, San Luis Valley, Colorado, Seviletta LTER, Socorro County, New Mexico, and Bandelier National Monument, Sandoval County, New Mexico. Examination of the type fits Muma's description but we were unable to determine if there was an error in labeling the type locality. None of the specimens from Utah that we used in the scaber study could be identified as *E. similis*. Females of this species have not been previously described.

Each of the above populations occurred in high desert shrub habitat and varied somewhat in color. The male population of Bandelier National Monument had a statistically significant variation in A/CP ratio indicating the possibility of sibling species. San Luis Valley (2303 m) specimens were collected in Rabbit Bush, snake weed, greasewood habitats. Bandelier National Monument specimens from Piñon-Juniper and Ponderosa Pine habitat and Sevilleta LTER from Piñon-Juniper habitat but not from grassland and creosote bush (Brookhart & Brantley 2000).

**Specimens examined.**—UNITED STATES: *Colorado:* Costillo & Saguache Counties, San Luis Valley, 8 June–8 August 1997, Jack & Irene Brookhart in wet pitfalls (22 ♂, 19 ♀); *New Mexico:* Socorro County, Sevilleta National Wildlife Refuge (34°03′N, 106°23′W), 1989–1994 in wet pitfalls (7 ♂, 18 ♀); Sandoval County, Bandelier National Monument (35°47′N, 106°18′W), 1998–2000 in wet pitfall traps (22 ♂, 19 ♀). Deposited at DMNS and University of New Mexico.

### *Eremobates actenidia* Muma 1989
Figs. 30, 59

*Eremobates actenidia* Muma 1989: 9–10, figs. 1, 2.

**Type.**—Male holotype from Gouldings Trading Post, Monument Valley, San Juan County, Utah, USA (37°06′N, 110°11′W), 2 June 1953, R.E. Ryckman, R.D. Lee, C.T. Ames, C.C. Lindt, C.T. Christianson. Deposited AMNH.

**Diagnosis.**—This specimen may be separated from all but *E. ctenidiellus* by its lack of ctenidia on the first post stigmatal segment. *Eremobates ctenidiellus* generally lacks ctenidia but can easily be distinguished by its pale coloration as opposed to the dark coloration of *E. actenidia* and the shape of the fondal notch, which is significantly longer than wide. It has a high A/CP ratio indicating longer appendages and a statistically thinner male fixed finger in relation to the fondal notch.

**Description.**—*Males:* Appendage and propeltidium coloration dusky yellow to brownish yellow, propeltidium tinged brownish violet on anterior and lateral margins, palpus tinged brownish violet on tarsus and metatarsus, legs dusky yellow. Cheliceral FF regularly curved, MF with small triangulate AT, no cleft, small IT with the posterior separate from the PT (Fig. 32), no ctenidia, 70 + palpal papillae. *Male holotype:* Total length 18.0, chelicera length 4.0, chelicera width 2.3, propeltidium length 2.3, propeltidium width 3.5, palpus length 17.0, first leg length 13.0, fourth leg length 20.0. *Ratios:* A/CP 7.94, CL/CW 1.74. PL/PW 0.66, FL/FW 1.02, FW/FFW 1.70, FW/CW 6.09. *Male measurements (4):* Total length 17.50–21.00, chelicera length 4.92–6.25, chelicera width 2.29–2.79, propeltidium length 2.17–2.83, propeltidium width 3.75–4.58, palpus length 16.5–22.0, first leg length 12.0–13.0, fourth leg length 19.5–23.0. *Ratios*: A/CP 5.94–6.78, CL/CW 2–2.42, PL/PW 0.58–0.68, FL/FW 0.79–1.06, FW/FFW 1.56–2.00, CW/FFW 6.09–8.13.

*Females:* Coloration as in male except the legs are lightly tinged violet at the tibia femur joint. Chelicera typical, MF with large PT, 2 IT, large AT, posterior IT in notch of PT, no cleft under AT, tiny to absent MST. Genital opercula with long, thin arms, a slightly curved interior margin ending in a lobe, wings offset, posterior margin truncate (Fig. 59).

*Female measurements (5):* Total length 16.0–20.5, chelicera length 4.8–5.8, chelicera width 1.8–2.4, propeltidium length 2.2–2.8, propeltidium width 3.2–4.4, palpus length 14.5–16.0, first leg length 9.5–11.0, fourth leg length 16.0–17.0. *Ratios:* A/CP 4.88–6.37, CL/CW 2.00–2.67, PL/PW 0.57–0.75, GOL/GOW 0.67–0.80.

**Remarks.**—*Eremobates actenidia* has only been found in the desert grass region of San Juan County, Utah. Brookhart collected from pitfall traps set in three different habitats along a 16 km stretch of Hwy 195 in San Juan County, Utah from 29 May 2000–28 August 2000 and again on 6 June 2001. *Eremobates actenidia* was collected from desert grasslands but not from desert shrub or Piñon-Juniper assemblages in this transect. *Eremobates mormonus* is found 161 km east in Montezuma County, Colorado and *E. corpink*, new species, is found 161 km west in the Coral Pink Sand Dunes of Kane County, Utah at approximately the same latitude.

**Specimens examined.**—UNITED STATES: *Utah:* San Juan County, 6.4 Km N of Bluff (37°17′N, 109°33′W), 10 June–26 August 2000, Jack & Irene Brookhart in wet pitfall traps (3 ♂, 4 ♀, DMNS).

***Eremobates socal*** new species
Figs. 10–16

**Types.**—Male holotype, female allotype; California, San Diego County, Mt. Palomar St. Park (33°20′N, 116°54′W), 13 July 1953, W.J. & J.W. Gertsch (AMNH).

**Etymology.**—A noun in apposition referring to the type locality, Southern California, as used by Jim Rome, radio and TV sports talk show host.

**Diagnosis.**—*Eremobates socal* can be separated from *E. zinni* and *E. mormonus* by size and shape of ctenidia, color variation and female genital operculum.

**Description.**—*Males:* Appendage and propeltidium background coloration dusky yellow, propeltidium violet brown on the anterior and lateral fringes, a broadly ovoid yellow center (Fig. 10), abdomen dusky grey, apical half of palpal metatarsus dusky violet, legs I & II dusky yellow, femur of legs III & IV dusky violet. Male cheliceral FF regularly curved, MF with large PT, small triangulate AT with a cleft, small IT, posterior IT separate from PT (Figs. 11–12), 47–60 palpal papillae, a few on tarsus (Fig. 13), 4 short needle like ctenidia extending less than half the succeeding segment (Fig. 14).

*Male holotype:* Total length 19.0, chelicera length 5.63, chelicera width 2.58, propeltidium length 2.50, propeltidium width 4.36, palpus length 18.0, first leg length 13.0, fourth leg length 21.5. *Ratios:* A/CP 6.46, CL/CW 2.18, PL/PW 0.57, FL/FW 1.00, FW/FFW 1.45, CW/FFW 5.64. *Male paratypes (4):* Total length 19.0–20.0, chelicera length 5.00–

5.63, chelicera width 2.42–2.58, propeltidium length 2.50–2.92, propeltidium width 4.17–4.38, palpus length 16.0–18.0, first leg length 12.0–14.0, fourth leg length 20.0–21.5. *Ratios:* A /CP 6.06–6.46, CL/CW 2–2.18, PL/PW 0.62–0.7. FL/FW 0.71–1.00, FW/FFW 1.17–1.70, CW/FFW 5.00–6.00.

*Females:* Coloration as in the male. Chelicerae typical with posterior IT of MF in the notch, no cleft under AT (Fig. 15). No palpal papillae, no ctenidia. Genital operculum with long, broad arms, long curved medial edge ending in a point, short, offset wings, curved posterior margin (Fig. 16).

*Female allotype:* Total length 19.0, chelicera length 5.29, chelicera width 2.08, propeltidium length 2.29, propeltidium width 3.83, palpus length 12.0, first leg 12.0, fourth leg length 19.0. *Ratios:* A/CP 5.27, PL/PW 0.60, CL/CW 2.54, GOL/GOW 0.72. *Female paratypes (2):* Total length 20.0–20.5, chelicera length 6.25–6.50, chelicera width 2.5, propeltidium length 2.5—2.6, propeltidium width 4.50–4.58, palpus length 14.5–15.0, first leg length 12.0, fourth leg length 18.0–19.0. *Ratios:* A/CP 5.97–6.00, CL/CW 2.5, PL/PW 0.57, GOL/GOW 0.5–0.6.

**Remarks.**—*Eremobates socal* is similar to *E. zinni* and *E. mormonus* but can be separated by the shape and size of the ctenidia, coloration, and shape of female genital opercula. It was found in the coastal shrub area on Mt. Palomar in San Diego County, California.

**Specimens examined.**—UNITED STATES: *California:* San Bernardino County, Big Bear Lake (34°14′N, 116°54′W), July 1950, no collector (♂, AMNH); Granite Cove, 8 Km N on Kelbaker Road (34°46′N, 115°39′W), E. Fasler (2 ♂, California State Riverside); Joshua Tree National Monument (35°07′N, 116°02′W), 22 August 1994, no collector (♀, DMNH); San Diego County, Mount Palomar State Park (now Palomar Mountain State Park) (33°20′N, 116°54′W), 13 July 1953, W.J. & J.W. Gertsch (3 ♂, ♀, AMNH).

*Eremobates zinni* Muma 1951
Figs. 27, 39, 50, 58

Muma 1951:58, figs. 65–68; Muma 1970:14; Muma 1987:1920.

**Type.**—Male holotype, female allotype from Las Vegas, Clark County (36°10′N, 115°08′W), Nevada in AMNH. Collected by Donald J. Zinn, May through August 1944. Female paratype from Las Vegas, Clark County (36°10′N, 115°08′W), Nevada, February through June 1945 (AMNH).

**Etymology.**—Named for the collector Donald Zinn.

**Diagnosis.**—*Eremobates zinni* is closely related to *E. socal* new species. It can be separated by the shape of the male chelicera, coloration, and shape of female genital opercula.

**Description.**—Males*:* Appendages dusky yellow with dusky violet brown on tarsus and distal end of metatarsus of palp, propeltidium dusky yellow with light violet tinges on anterior and anterio-lateral edges (Fig. 50). Male cheliceral FF regularly curved, MF with small triangulate AT with cleft, posterior IT separate from PT; fondal notch longer than wide (Fig. 27). Ctenidia 4 short, flat (Fig. 39), 40–80 palpal papillae.

*Male holotype:* Total length 21.0, chelicera length 5.7, chelicera width 2.5, propeltidium length 3.0, propeltidium width 6.4, palpus length 19.0, first leg length 15.0, fourth leg length 23.0. *Ratios:* A/CP 6.55, CL/CW 2.28, PL/PW 0.47, FL/FW 1.17, FFW/FW 1.33, CW/FFW 0.80. *Male measurements (1):* Total length 14.0, propeltidium length 3.12, propeltidium width 6.4, chelicera length 6.24, chelicera width 3.0, palpus length 12.0, first leg length 10.0, fourth leg length 16.0. *Ratios:* A/CP 4.10, CL/CW 2.08, PL/PW 0.49, FL/FW 0.90, FFW/FW 1.38, CW/FFW 1.10.

*Females:* Same coloration as males, MF with posterior IT in the notch of PT, AT with no cleft, genital opercula with long, thin arms, a curved medial edge ending in a point, short offset wings and a curved posterior surface (Fig. 58). *Female allotype:* Total length 23.0, propeltidium length 3.9, propeltidium width 7.0, chelicera length 4.8, chelicera width 2.5, palpus length 15.0, first leg length 13.0, fourth leg length 21.0. *Ratios:* A/CP 4.80, CL/CW 2.52, PL/PW O.56, GOL/GOW 0.68.

**Remarks.**—*Eremobates zinni* and *E. ascopulatus* are sympatric at the Nevada Test Site. *Eremobates zinni* appears to be related to both *E. socal* new species and *E. corpink* new species.

**Specimens examined.**—UNITED STATES: *Nevada:* Clark County, Las Vegas (36°10′N, 115°08′W), May–August 1944, Donald J. Zinn (♂, AMNH). *Utah:* Washington County, Saint George (37°06′N, 113°35′W), no date, no collector (♂, BYU).

*Eremobates corpink* new species
Figs. 20–26

**Type.**—Male holotype from Kane County, Utah, Coral Pink Sand Dunes (37°05′N, 112°40′W), 2 August 1988, R.W. Bauman (DMNH). Female allotype from Kane County, Utah, Coral Pink Sand Dunes, 11 June 2002, S.M. Clark (DMNS). One male paratype from Kane County, Utah, Escalante National Monument (37°25′N, 111°33′W), 9 July 2000, D.J. Craven, E. Cygen and W.N. Wendel (BYU). One male from Kane County, Utah, Coral Pink Sand Dunes, 9 July 2002, S.H. Clark and J.S. Robertson (BYU).

**Diagnosis.**—Separated from *E. zinni* and *E. ascopulatus* by size and shape of ctenidia, shape of female opercula and coloration.

**Etymology.**—A noun in apposition referring to the Coral Pink Sand Dunes, Kane County, Utah.

**Description.**—Males*:* Overall coloration pale straw yellow, palpal tarsus and distal one third of metatarsus blotched brownish violet, all other appendages pale straw yellow, propeltidium with lightly blotched brownish violet except for pale median ovoid region (Fig. 20), abdomen yellow to grey. Cheliceral fixed finger thin, regularly curved, movable finger with large PT, smaller triangulate AT, cleft anterior to AT, posterior IT separate from PT (Figs. 21–22). Two short, thin ctenidia (Fig. 24), palpal papillae 40–82 (Fig. 23). *Male holotype:* Total length 21.0, propeltidium length 2.5, propeltidium width 2.9, chelicera length 4.7, chelicera width 2.4, palpus length 16.0, first leg length 12.5, fourth leg length 22.0. *Ratios:* A/CP 6.92, PL/PW 0.90, CL/CW 1.96, FL/FW 0.56, FFW/FW 1.80, CW/FFW 12.00. *Male paratypes (2):* Total length 20.0–20.5, propeltidium length 2.60–3.82, propeltidium width 3.15–3.90, chelicera length 3.82–5.45, chelicera width 2.0–3.9, palpus length 16.0–17.5, first leg length 12.0–14.0, fourth leg length 22.0–22.5. *Ratios:* A/CP 6.22–6.94, PL/PW 0.80–0.98, CL/CW 1.32–2.60, FFW/FW 1.19–1.45, FL/FW O.56–0.94, CW/FFW 7.96–10.70.

*Female allotype:* Overall coloration as in male, palpus and legs yellow, propeltidium blotched violet purple in anterior edge, abdomen grey, chelicera typical, no cleft under AT of MF, posterior IT in notch of PT of MF (Fig. 25), 2 faint violet stripes on posterior dorsal edge of chelicera, genital opercula with short, broad arms, slightly curved medial edge with two small lobes, wings short and curved, posterior edge curved (Fig. 26). *Female allotype:* Total length 19.0, propeltidium length 2.5, propeltidium width 2.8, chelicera length 6.0, chelicera width 2.8, palpus length 15.0, first leg length 12.0, fourth leg length 20.0. *Ratios:* A/CP 5.53, CL/CW 2.15, PL/PW 0.90, GOL/GOW 0.73.

**Remarks.**—*Eremobates corpink* appears related to *E. zinni*. The restricted habitat in and around the Coral Pink Sand Dunes has produced other endemic species (Knisley & Hill 2001).

**Specimens examined.**—UNITED STATES: *Utah:* Kane County, Escalante National Monument (37°25′N, 111°33′W), 9 July 2000, D.J. Craven, E. Cygen, & W.N. Wendel (♂ paratype, BYU); Coral Pink Sand Dunes (37°02′N, 112°42′W), 9 July 2002, S.H. Clark & J.S. Robertson (♂ paratype, BYU).

*Eremobates legalis* Harvey 2002
Fig. 60

*Datames geniculatus* (C.L. Koch) Simon 1879:138. (Not *E. geniculatus* Simon, *sensu* Muma 1951).
*Eremocosta geniculata* (Simon) Roewer 1934:570.
*Eremobates legalis* Harvey 2002:451.

**Type.**—Female holotype from Mexico, No. 2129 (Roewer No. 9135) in MNHN

**Etymology.**—From the Latin "legalis" which means according to the law (Harvey 2002). The original specific epithet of "geniculatus" is from the Latin meaning bent. This origin is interesting since it probably refers to the male fixed finger and *E. geniculatus* is known only from one female.

**Diagnosis.**—Muma (1970) distinguishes this species by the presence of two small ctenidia but this is invalid since females of several species possess ctenidia. Female genital operculum is similar to *E. ascopulatus*.

**Description.**—*Female:* Overall coloration pale yellow. Palpus, legs yellow, propeltidium with faint violet tinge anteriorly. Abdomen grey. Chelicera typical, posterior tooth of MF in the notch of PT, no cleft. No palpal papillae, two tiny hair like ctenidia. Operculum with long, thin arms, smooth medial margin, short gently curving wings, posterior margin curved (Fig. 60). *Female holotype:* Total length 23.0, chelicera length 5.4, chelicera width 2.5, propeltidium length 2.3, propeltidium width 4.3,

palpus length 13.0, first leg length 10.5, fourth leg length 14.5. *Ratios:* A/CP 4.93, CL/CW 2.16, PL/PW 0.53, GOL/GOW 0.69.

**Remarks.**—Simon's (1879) description of *Datames geniculatus* was of a specimen differing from Roewer's 1934 description of *Eremocosta geniculata*. Harvey clarified this in 2002 by designating the type (Roewer No. 9135) *Eremobates legalis*. *Eremobates legalis*/*E. geniculatus* is known from the type only. Muma (pers. comm.) indicates that the other specimen in the vial is an immature. It is the only member of the scaber group presently known from Mexico (Vásquez 1981; Muma 1987). We have examined other specimens from the southwestern United States labeled *E. geniculatus* by Muma but now consider them misidentifications.

## KEY TO THE MALES OF *EREMOBATES SCABER* GROUP

(Females can best be distinguished by the shape of genital opercula)

1. Ctenidia none or hair-like ..... 2
   Ctenidia present ..... 3
2. Ctenidia absent, palpal tarsus, metatarsus brownish violet ..... *Eremobates actenidia*
   Ctenida absent or 2 hair-like (Fig. 38), palpal tarsus and metatarsus pale ..... *Eremobates ctenidiellus*
3. Two ctenidia present ..... 4
   More than two ctenidia present ..... 8
4. Fixed finger severely crimped in ectal view (Fig. 1); ctenidia short, thin, pointed (Fig. 42); palpus dusky straw yellow ..... *Eremobates scaber*
   Fixed finger with no or slight crimping in ectal view; ctenidia variable; palpus variable 5
5. Overall coloration lemon yellow; ctenidia flat, sword-shaped (Fig. 40) ... *Eremobates hodai*
   Overall coloration dusky yellow, brown or brownish violet; ctenidia not sword-shaped .. 6
6. Palpal color dusky yellow; posterior intermediate tooth separate from principle tooth of movable finger; no cleft under anterior tooth of movable finger; fond length and width equal (Fig. 35); ctenidia flat, needle-like (Fig. 43) ..... *Eremobates ascopulatus*
   Palpal color dusky yellow to brownish violet; posterior intermediate tooth in the notch of primary tooth of movable finger; cleft under anterior tooth of movable finger; fond length to width ratio equal or wider; ctenidia variable ..... 7
7. Palpal color dusky yellow; cleft under anterior tooth of movable finger; fond length to width ratio equal (Fig. 33); ctenidia broad, flat (Fig. 36) ..... *Eremobates clarus*
   Palpal coloration brown violet on tarsus and metatarsus; cleft under anterior tooth of movable finger; fondal notch wider than long; ctenidia short, thin ..... *Eremobates corpink*
8. Anterior tooth of movable finger absent or an undifferentiated ridge; fondal notch longer than wide (Fig 5); four flat ctenidia (Fig. 7) ..... *Eremobates icenoglei*
   Anterior tooth of movable finger present; fondal notch ratio equal or wider; three or four ctenidia, thin or flat ..... 9
9. Ctenidia flat ..... 10
   Ctenidia thick, needle-like ..... 11
10. Three to four ctenidia present, stiletto-like, extending half the length of succeeding sternite (Fig. 39); palpal tarsus and distal end of metatarsus dusky; posterior intermediate tooth of movable finger separate from principle tooth; cleft under anterior tooth of movable finger (Fig. 27) ..... *Eremobates zinni*
    Four, flat ctenidia present (Fig. 37); palpal tarsus and metatarsus dusky amber; posterior intermediate tooth of movable finger in notch of primary tooth; no cleft under anterior tooth of movable finger (Fig. 29) ..... *Eremobates mormonus*
11. Four to six thin, short, hair-like ctenidia present (Fig. 41); no palpal papillae; palpus brownish violet on tarsus, metatarsus, tibia, and tib-fib joint; posterior intermediate tooth of movable finger in the notch of principle tooth; no cleft under anterior tooth (Fig. 28) ... ..... *Eremobates similis*
    Four, flat ctenidia present (Fig. 14); papillae present (Fig. 13); palpus dusky brown on

tarsus and metatarsus; posterior tooth separate from principle tooth of movable finger; cleft under anterior tooth of movable finger (Fig. 11) ..... *Eremobates socal*

## CLADISTIC ANALYSIS

To our knowledge, no previous cladistic analysis has been attempted for any genus or species group of Solifugae. Herein we present the first testable hypothesis of the relationships among species in the *E. scaber* species group (Fig. 61) with a member of the *Eremobates pallipes* species group, *E. pallipes* (Say 1823) set as the outgroup based on the simple structure of male chelicera and female genital opercula. Many of the ratios that are useful as diagnostic characters, are too variable to be useful as characters for cladistic analysis. We limited our cladistic analysis to characters that could be coded objectively.

The following 12 characters were used to analyze the relationships among the species in the *E. scaber* species-group (see Table 1). 1 'Propeltidium color': [0] no color, [1] color halfway down, [2] color down sides. 2 'Number of ctenidia': [0] zero, [1] two, [2] four. 3 'Ctenidia shape': [0] NA, [1] flat, [2] peg, [3] thin. 4 'Ctenidia length': [0] NA, [1] short, [2] medium, [3] long. 5 'Presence/absence palpal papillae': [0] present, [1] absent. 6 'Palpal coloration': [0] pale or dusky, [1] dark tibia and metatarsus, [2] dark tarsus, metatarsus, tibia, and femur. 7 'PIT': [0] separate, [1] in notch, [2] NA. 8 'FF crimped': [0] no crimp, [1] crimped. 9 'Cleft AT: [0] no, [1] yes, [2] NA. 10 'Size AT': [0] small, [1] large, [2] NA. 11 'GO shape': [0] smooth, [1] undulate, [2] hooked. 12 'MST': [0] medium, [1] tiny, [2] absent.

We used PAUP version 4.0 beta (Swofford 2002) to analyze the data. All characters were unordered and given equal weight. We used the branch and bound (b and b) technique to search for the most parsimonious trees resulting in one tree (Fig. 61) with a length of 38, a consistency index of 0.63 and a retention index of 0.68. Characters were then reweighted by the maximum value of the consistency indices resulting in the same tree. However, the length was reduced to 24, the consistency index was 0.68 and the retention index was 0.73. When the characters were reweighted, three characters (2, 5 & 8) had a weight of 1; six characters (1, 4, 7, 9, 10 and 11) had a weight of 0.67; two characters (3 & 12) had a weight of 0.5; and character 6 had a weight of 0.4. Although our cladistic analysis resulted in one best tree, the relatively low consistency index and the relatively few characters deemed useful for the cladistic analysis points to the need for exploring the use of molecular markers in future phylogenetic analyses of solifugids.

## DISCUSSION

Characters previously utilized by Muma, i.e. coloration, number and shape of ctenidia, number of palpal papillae, length (depth) versus width of fondal notch were valuable characters for differentiating species although statistical analysis of the FL/FW ratio character demonstrates that in several species there is more variability than Muma indicates. In addition the shape of the anterior tooth on the movable finger of the males, the presence and size of the mesal tooth and the position of the posterior intermediate tooth of the movable finger relative to the movable finger on both males and females was important. Some species also had a consistent cleft underneath the anterior tooth of the MF caused either by a depression of the dorsal edge of the FF or a slight ridge that formed anterior to the AT of the FF. Shape of male fixed finger from an ectal view was also important with some displaying an upward undulation or "crimp" and others a more normally rounded appearance. Figures 27–35 demonstrate variability and are presented for comparison purposes.

In those populations in which sufficient specimens were available for examination there was some variation in the shape and number of ctenidia but useful general criteria could be established. Some members of the same species had ctenidia that were bifed while the rest were pointed or blunt, probably because of wear. Infrequently some ctenidia were bent (see Figs. 36–43 for comparison). Some female groups displayed ctenidia but in all cases they were thin and short (Fig. 44). We did not find them to be diagnostic. We examined penultimate specimens of *E. similis* from Sevilleta LTER for ctenidia but found none. In those species in which palpal papillae are part of the diagnosis there was some var-

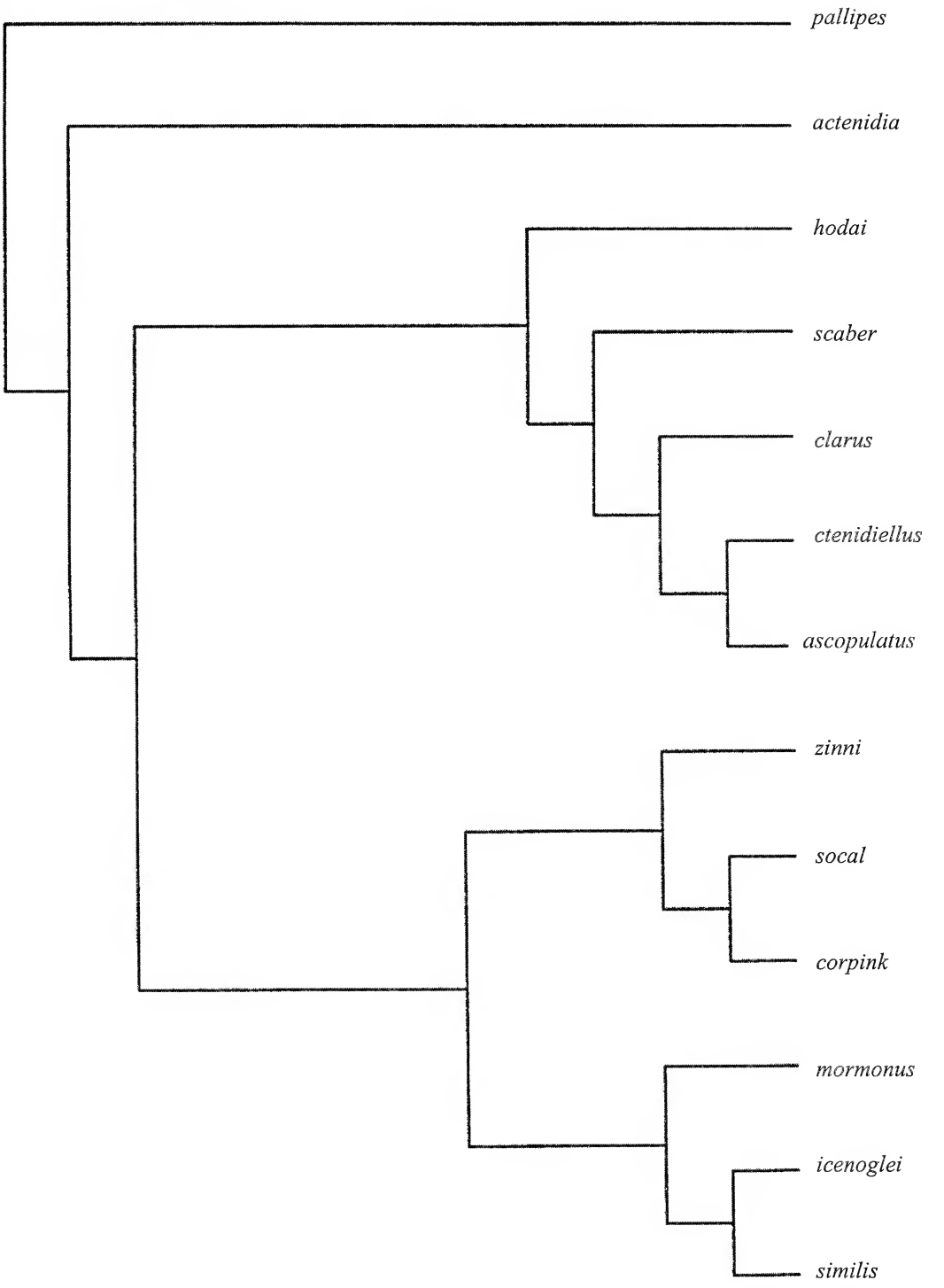



Figure 61.—Cladogram (using Paup 4.0) of the *Eremobates* species group with a length of 24, a consistency index of 0.68 and a retention index of 0.73, after character reweighting (see text for details). *Eremobates pallipes* was used as the outgroup.

Table 1.—Character matrix for species of the scaber group of the genus *Eremobates* with *E. pallipes* (Say 1823) as the outgroup. See text for description of characters.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *E. pallipes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *E. scaber* | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 |
| *E. hodai* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| *E. clarus* | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 |
| *E. ctenidiellus* | 2 | 1 | 3 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| *E. ascopulatus* | 2 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| *E. zinni* | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 2 |
| *E. socal* | 2 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 1 |
| *E. icenoglei* | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 0 | 2 | 2 | 2 | 0 |
| *E. mormonus* | 1 | 2 | 3 | 3 | 0 | 1 | 1 | 0 | 0 | 1 | 2 | 1 |
| *E. corpink* | 2 | 1 | 3 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 1 |
| *E. actenidia* | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *E. similis* | 1 | 2 | 3 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 2 | 1 |

iation among the number of palpal papillae including an occasional complete absence. There is some evidence that papillae arise sequentially after the last molt.

Propeltidium coloration was also helpful in identifying several species. Many species had light brownish violet mottling on the anterior edge but several also had distinctive color patterns (see Figs. 45–51). The use of coloration in solifugids captured in pitfall traps and preserved in alcohol should be approached with caution although this trait is used in this study. Material from Hanford, Washington contained both light and dark specimens in the same vial. Solifugids collected in wet pitfall traps from San Luis Valley, Colorado changed color over a two year period (Brookhart, pers. obs.). Female coloration was almost always the same as the males. Female genital opercula were quite species specific (Figs. 52–60).

Male ratios of A/CP, FL/FW, FW/FFW proved to be statistically significant for some species. Using the Tukey-Kramer analysis of variance we found *E. similis* and *E. mormonus* to be long legged species and *E. hodai* to be a short legged species. All others showed no significant statistical difference. Only *E. icenoglei* proved to have a longer FL/FW ratio and *E. similis* and *E. mormonus* were wider. The FW/FFW ratio identifies those species with wider or thinner fixed fingers. Those with significant differences were *E. actenidia* with a thin FF and *E. clarus*, *E. icenoglei*, and *E. scaber* with wider FF. All were significant at the 95% level of confidence. PL/PW and CL/CW showed no significance. No statistically significant character was found among any of the female ratios tested. Species vary in the position of the posterior intermediate tooth relative to the primary tooth of the movable finger and the presence or absence of a cleft anterior to the anterior tooth of the movable finger.

Brookhart & Muma (1981, 1987) and Muma & Brookhart (1988) demonstrated that solifugids are generally allopatric or in the case of the *Eremobates palpisetulosus* group sympatric for two species. Our study indicates that members of the scaber group are allopatric except *E. ascopulatus* and *E. zinni*. Our cladistic analysis seems to demonstrate a northern and a southern clade (compare the cladogram in Fig. 61 with the map in Fig. 62). Males in the northern clade have two ctenidia, a more pronounced "crimp" in the fixed finger of the male and females with either smooth or undulate medial margin of the genital operculum. Their range is larger than the southern group which has species with more endemic status. Southern males have four ctenidia, a more smoothly curved fixed finger, and females have a hooked process at the juncture of the medial margin and the wing of the genital operculum. The sympatry between *E. zinni* and *E. ascopulatus* may reflect a connection within the Lahontan Basin. We do not have enough data to indicate whether there is a temporal separation or some other process of niche partition.

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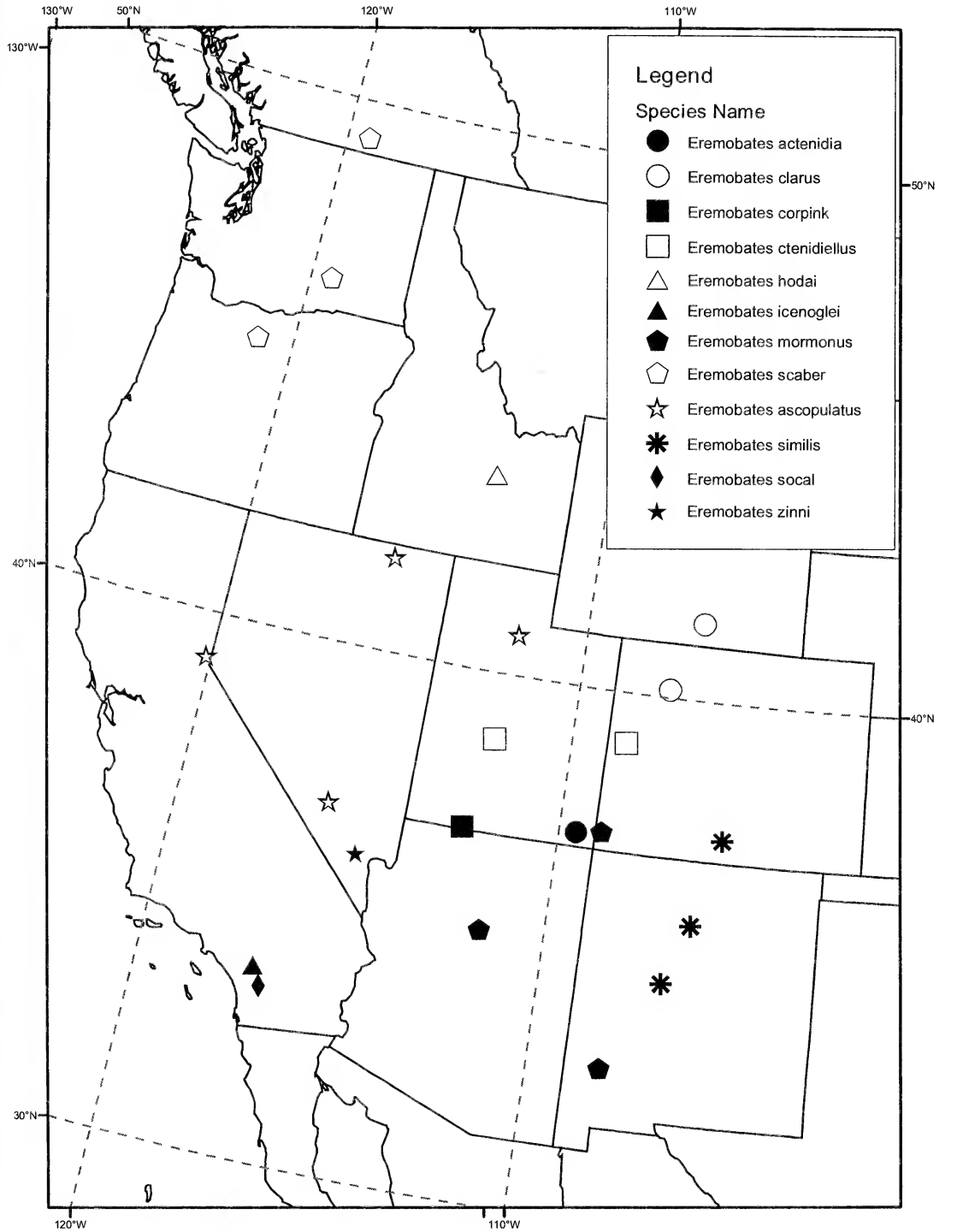


Figure 62.—Map of *Eremobates scaber* group species.

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# ASSEMBLAGES OF SPIDERS ON MODELS OF SEMI-ARID SHRUBS

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**ABSTRACT.** Many environmental factors influence the composition of animal assemblages. For spider assemblages, plant architecture is an important variable. Here we examine the effects of various plant architectural attributes by using models of shrubs in which we control branch orientation (horizontal or vertical) and height above the ground (0, 10, or 40 cm). Guild membership, based on hunting strategy (jumpers, pursuers, ambushers, or trappers), was used to characterize spider assemblages. Five replicates of the six treatments (two orientations by three heights) were randomly placed in a 60 m by 50 m grid among big sagebrush in a shrub-steppe habitat and sampled at 3 week intervals from July–October in 1997 and 1998. ANOVA was used to demonstrate that not only do single architectural variables influence the distribution of spiders but also the interaction of architectural variables influence spider distribution. Differences in the assemblages of spiders on the models were the result of architecture differences. Jumpers selected horizontal, 10 cm models and pursuers selected vertical, 0 cm models. Trappers were most abundant on horizontal, 0 cm models.

**Keywords:** Community ecology, plant architecture, shrub-steppe

The distributions of a wide variety of organisms are influenced by structural characteristics of their physical environment (MacArthur 1958; Wilson 1974; Rotenberry & Wiens 1980; James & Wame 1982; Landres & MacMahon 1983; Vander Wall & MacMahon 1984; Southwood 1996). In particular, plant attributes correlate with animal species diversity (Schoener 1968; Pianka 1973; Lawton 1986).

Spiders have been the focus of many community ecology studies because they are generalist carnivores, many species live in the same habitat and they are easily collected (Wise 1993). Several habitat structures correlate with spider abundance and diversity (Colebourn 1974; Gibson et al. 1992; Johnson 1995; Halley et al. 1996). Plant architecture was the specific subject of many studies (Fautin 1946; Chew 1961; Allred & Beck 1967; Allred 1969; Chaplin 1976; Gunnarsson 1988; 1990, 1996; Janetos 1986; Ward & Lubin 1992; Wise 1993; Sundberg & Gunnarsson 1994; Aiken & Coyle 2000; Ysnel & Canard 2000; Raizer & Amaral 2001).

The effect of plant architecture on the distribution of spiders on big sagebrush (*Artemisia tridentata*) has been the focus of several studies. Architectural features, such as herb height and shrub size were associated with the distribution of spiders (Abraham 1983). Changes in the density of individual big sagebrush altered the composition of the spider community (Hatley & MacMahon 1980; Wing 1984). Robinson (1981) and Ehmann (1994c) used models to simulate big sagebrush density, substrate diameter and horizontal and vertical orientation.

Guilds, based on mode of feeding (Root 1967), are widely used as dependent variables in studies of spider assemblages (Chew 1961; MacMahon 1973; Uetz 1977; Moran & Southwood 1982; Hurd & Eisenberg 1990; Pettersson 1996; Mason et al. 1997). Guild analysis provides a way to examine the organization of spider communities on big sagebrush (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984; Ehmann 1994a). Previous studies suggest that the guild composition of spider assemblages on big sagebrush is predictable despite differences in species

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composition (Abraham 1983; Ehmann 1994a). Although jumpers are ubiquitous and are found on the ground and on most vegetation, they dominate the spider assemblages found on big sagebrush. In the guild classification used by Ehmann, the spider community on big sagebrush was divided into four guilds (trappers, jumpers, ambushers and pursuers) using hunting strategy as a means of identifying guild membership. Trappers, including Araneidae, Dictynidae, Linyphiidae, Tetragnathidae and Theridiidae, construct webs to trap prey. Jumpers, Oxyopidae and Salticidae, actively seek prey using their well developed sense of sight to pounce on prey from a distance. Ambushers, Thomisidae, are sit-and-wait predators that wait for prey to move within striking distance. Pursuers, including Anyphaenidae, Clubionidae, Gnaphosidae, Lycosidae and Philodromidae, are active predators that run down prey.

In this study, the distribution of spiders by guild and a possible mechanism for the observed patterns were addressed using an experimental approach in the well-studied spider assemblage on big sagebrush. Two shrub characteristics stand out as making them architecturally different than the surrounding plants in shrub-steppe ecosystems. They are taller and they have more horizontal plant components. Shrub height has been associated with differences in spider community composition (Hatley & MacMahon 1980; Abraham 1983; Greenstone 1984; Döbel et al. 1990; Gibson et al. 1992 ; Lubin et al. 1993; Ward & Lubin 1993; Aiken & Coyle 2000; McReynolds 2000). Robinson (1981) used simple models to demonstrate that vertical/horizontal orientation affected the distribution of certain spider species. In this study, artificial shrubs were used to manipulate height and orientation of pseudobranches to determine the roles these two variables play in the distribution of spiders affiliated with specific guilds. Data from a four-year census of spiders on big sagebrush in the same area as the experiment were used to interpret results in relation to the natural system.

The specific purpose of this study was to measure the distribution of spiders affiliated with each of four guilds on models that simulated two plant architectural variables: height and branch orientation. Spider abundance on each model served as the dependent variable in the analyses.

## METHODS

**Site.**—This study was conducted at a 10 ha site 3.7 km east and 0.9 km north of the Hyde Park, Utah post office (NW1/4 SW1/4 sec 6, T 12 N, R 2 E, Salt Lake Meridian) at an elevation of 1755 m. The site was dominated by big sagebrush and grass with alfalfa fields on the east and west margins and steep canyons on the north and south. The experiment took place on the south side of a farm road that divided the site. This area has a southwest aspect and 5% slope. The part of the site north of the road was used for a four-year census. This site is 4 km north of the area used by Hatley and MacMahon (1980), Robinson (1981), Abraham (1983), and Wing (1984) and 7.5 km northwest of Ehmann's site (1994a).

**4-year census.**—An 80 $m^2$ grid was established and divided into quadrants to facilitate locating sampling points. The four corners, midpoints of each side and the center were permanently marked. In 1995, 20 shrubs were chosen for the census for each sampling day. After 1995 the number of shrubs sampled per day was increased to 24. Spiders were collected every 14–28 d from May until October in 1995–98. The number of sample days ranged from 7–13 totaling 42 for the four years. For each census day, five or six points within the grid were selected using a table of random numbers to identify the coordinates of the points. Sampling began 2 h after sunrise using the randomly selected coordinates. The four big sagebrush closest to the sampling point and meeting the established criterion (0.75–1.5 m high) were noted. The height criterion was established in order to sample similar sized big sagebrush because there is a positive relation between shrub size and spider abundance (Abraham 1983).

Spiders were collected from each shrub by using a beating sheet technique (Southwood 1978; Ehmann 1994a). Large spiders were captured by hand using vials and small spiders were captured with an aspirator. The beating sheet technique captures about 84% of the spiders on big sagebrush and the capture rate represents an unbiased sample of species found on the shrubs (Ehmann 1994b). Ehmann also showed that their was no effect on the sub-

Figure 1.—Photograph of model in horizontal orientation.

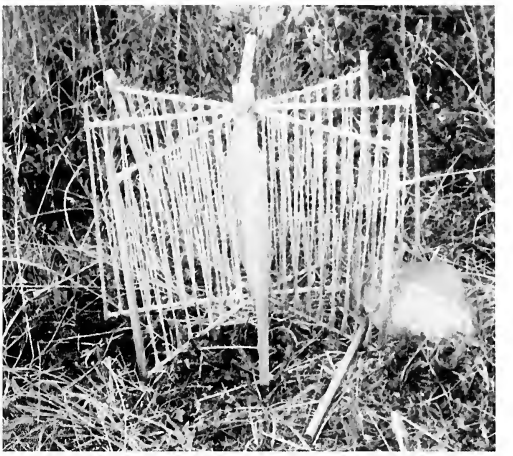

Figure 2.—Photograph of model in vertical orientation.

sequent sampling of the same shrub after a two-week interval. All spiders captured from a shrub were immediately placed in a vial with 70% ethanol for preservation. This process continued until the four shrubs around the first point were sampled. The second point was then located and the process repeated until all 24 shrubs were sampled.

Spiders were sorted by species and identified using the reference collection of Cache Valley spiders at Utah State University (Ehmann 1994b). Data were recorded as total species abundance and guild abundance per day. Guild assignments (jumpers, pursuers, ambushers, and trappers) followed the procedures used by Ehmann (1994a). Specimens were deposited in the Utah State University Entomology Collection. A pre-experiment census was also conducted, in the same manner, for one season (1997) in the area where the experimental models were placed.

The Jaccard index, a coefficient of similarity that gives an indication of the degree to which species composition overlaps between two locations (Southwood 1978), was used to compare assemblages of spiders in the experiment with the natural distribution found on big sagebrush.

**Experiment with models.**—The models for the experiment were constructed from wood and sisal twine and in some cases aluminum conduit (Figs. 1 & 2). A center post was the "trunk." A "whorl" of eight dowels "branched" perpendicularly from each end. A wooden slat was used to keep the ends of the branches 40 cm apart. Sisal twine wrapped around the dowels was used to represent smaller branches. The models were cylinders with 63 cm diameters, 40 cm heights and volumes of 124,690 $cm^3$ (Heikkinen 2001). Shrub volumes measured in previous studies were 24,991–598,796 $cm^3$ (Hatley & MacMahon 1980) and 120,000–311,000 $cm^3$ (Wing 1984). Two orientations were tested (vertical and horizontal) by turning the model 90° on its longitudinal axis.

Three height positions were used for each of the vertical/horizontal orientations. One treatment was placed on the ground. In the second and third treatments aluminum conduit was used to raise the model 10 cm and 40 cm off the surface. The conduit was driven into the ground and then inserted in a hole drilled into the center post. Five replicates of each treatment were established on a 10 m by 10 m grid. Treatments were assigned to each point on the grid by random draw. Once a treatment was assigned to a point, it remained at that point for the year, but a second random assignment took place for the second year. Where sample points coincided with a shrub, the model was placed as close to the sample point as possible without touching a shrub.

Data were collected in 1997 and 1998 beginning in the last week of July and ending in mid-October. Spiders were collected from the models every 3 weeks using the beating sheet technique, and preserved in 70% ethanol. Specimens were sorted and identified in the laboratory and assigned to one of the four

guilds using the same procedures described above.

Data were analyzed using ANOVA (SAS 1982) where species the independent variable was an individual spider and the dependent variables were the spider's guild, the orientation of the model on which it was found, and the height of the model. All two-way and three-way interactions were tested.

## RESULTS

**Censuses of spiders on big sagebrush at Hyde Park.**—A baseline for the interpretation of these experiments was established from censuses of spiders found on big sagebrush from 1995–1998 (Table 1). The jumper guild was most abundant each year containing 62.0% of the total individuals (range = 57.5–66.0%). Four jumpers were among the ten most abundant species across all guilds. *Pelegrina aeneola* Curtis 1892, a jumper, was most abundant accounting for 26.9% of the total. Other abundant jumpers were *Sassacus papenhoei* Peckham & Peckham 1895, *Oxyopes scalaris* Hentz 1894 and *Phidippus johnsoni* Peckham & Peckham 1883. The trapper guild was second most abundant with 21.1% of the individuals collected and it had three of the ten most abundant species: *Theridion petraem* L. Koch 1872, *T. neomexicanum* and *Metapeira foxi* Gertsch & Ivie 1936. Pursuers was the third most abundant guild with 12.9% of the total. The most abundant pursuers were *Philodromus histrio* Latreille 1819 and *Tibellus oblongus* Walckanaer 1802. Ambushers was the least abundant guild with only 2.9% of the spiders collected. One ambusher, *Xysticus gulosus* Keyserling 1880, was the tenth most abundant species.

**Results of the experiment with models.**—The Jaccard index yielded a similarity value of 0.55 between the Hyde Park census and the experiment. See Table 1 for a list of the species found in the census and the experiment.

Our principle hypothesis was that jumpers would be most abundant on shrub-like models, i.e., 40 cm models placed in a horizontal orientation. Since this was an experimental manipulation of two shrub variables which may effect the distribution patterns of all spider guilds, the significance of all variables (height, orientation and guild affiliation) and higher-order interactions were identified using ANOVA (Table 2).

Two variables were significant by themselves. Over half of all spiders collected were jumpers and about half of all spiders were on the 0 cm models (Table 3).

Although the assemblages of spiders based on guild membership from the censuses and the experiment were similar (Fig. 3), there were differences in the species composition of the assemblages. Jumpers was the most abundant guild in both cases (65.8% and 51.6%), however, *Pelligrina aeneola* was most abundant in the census, but accounted for only 1.4% of all spiders on the experimental models. Although pursuers were third most abundant in both treatments, they accounted for 11.0% of the spiders in the census, but 19.4% of the spiders collected from the experimental models. *Philodromus histrio* was the most abundant pursuer in the census (4.8%), but was only 0.2% of the spiders collected from the experimental models. *Tibellus oblongus* was more abundant on the experimental models: 17.9% vs. 4.2%.

The significant variables identified by the ANOVA only indicate that spiders are reacting differentially to architectural variables. Two-way interactions were examined to elucidate differences in spider distribution by guild based on differences in height or orientation. Even though orientation was not significant alone, height by orientation was also included because the complete model was analyzed. All two-way interactions were significant.

The guild by height interaction was significant because 86% of the pursuers and 44% of the trappers were on the 0 cm models. Orientation by itself was not a significant variable, about half were on models of each orientation; the interaction of orientation with guild and height was significant. Jumpers were more abundant on horizontal models (58%) and pursuers were more abundant on vertical models (81%). The height by orientation interaction was significant because 61% of the spiders on the 10 cm models were on horizontal ones and 57% of spiders on the 0 cm models were on vertical ones.

The three-way interaction was the analysis used to test our principle hypothesis that spiders belonging to specific guilds would be more likely to be found on specific models. For example, jumpers would be most abundant on tall, horizontal models. The three-way

Table 1.—Abundance of spider species found at Hyde Park and on the experimental models.

| Species | Census | | | | Experiment | |
|---|---|---|---|---|---|---|
| | 1995 | 1996 | 1997 | 1998 | 1997 | 1998 |
| *Sassacus papenhoei* | 267 | 707 | 143 | 196 | 19 | 31 |
| *Pelegrina aeneola* | 251 | 966 | 433 | 717 | 4 | 2 |
| *Phidippus johnsoni* | 49 | 121 | 42 | 58 | 14 | 20 |
| *Evarcha hoyi* | 15 | 10 | 39 | 63 | 1 | 1 |
| *Habronattus hirsutus* | 13 | 15 | 1 | 0 | 0 | 0 |
| *Tutelina similis* | 2 | 12 | 4 | 19 | 2 | 4 |
| *Pellenes hirsutus* | 3 | 27 | 5 | 10 | 0 | 4 |
| *Synagales idahoansis* | 0 | 12 | 1 | 1 | 0 | 1 |
| *Talavera* sp. | 0 | 2 | 2 | 6 | 0 | 1 |
| *Oxyopes scalaris* | 221 | 628 | 81 | 306 | 44 | 85 |
| Salticidae | 0 | 10 | 4 | 0 | 0 | 2 |
| Jumpers | 821 | 2510 | 755 | 1376 | 74 | 147 |
| *Philodromus histrio* | 68 | 235 | 53 | 181 | 0 | 1 |
| *Philodromus rufus* | 0 | 24 | 5 | 4 | 1 | 0 |
| *Philodromus sp.* | 0 | 1 | 1 | 1 | 0 | 0 |
| *Tibellus oblongus* | 71 | 188 | 58 | 95 | 33 | 44 |
| *Ebo evanses* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Thanatus formicinus* | 2 | 0 | 0 | 0 | 0 | 0 |
| *Cheiracanthium inclusum* | 5 | 74 | 23 | 23 | 2 | 2 |
| *Anyphaena pacifica* | 1 | 3 | 1 | 0 | 0 | 0 |
| *Zelotes subterraneus* | 3 | 0 | 0 | 1 | 0 | 0 |
| Gnaphosidae | 5 | 1 | 1 | 2 | 0 | 0 |
| Clubionidae | 0 | 1 | 1 | 2 | 0 | 0 |
| Unknown pursuer | 0 | 1 | 1 | 0 | 0 | 0 |
| Pursuers | 155 | 528 | 144 | 310 | 36 | 47 |
| *Xysticus gulosus* | 21 | 116 | 12 | 28 | 5 | 7 |
| *Xysticus cunctator* | 0 | 2 | 0 | 0 | 0 | 0 |
| *Xysticus montanensis* | 2 | 1 | 0 | 0 | 0 | 0 |
| *Xysticus* sp. | 2 | 0 | 0 | 1 | 0 | 0 |
| *Misumenops lepidus* | 26 | 6 | 7 | 13 | 1 | 2 |
| *Misumenoides* sp. | 0 | 0 | 1 | 0 | 0 | 0 |
| *Coriarchne utahensis* | 6 | 2 | 2 | 4 | 0 | 1 |
| Ambushers | 57 | 127 | 22 | 46 | 6 | 10 |
| *Theridion petraeum* | 124 | 305 | 142 | 229 | 9 | 42 |
| *Theridion neomexicanum* | 36 | 61 | 104 | 57 | 11 | 1 |
| *Theridion differens* | 0 | 0 | 1 | 4 | 0 | 0 |
| *Theridion* sp. | 25 | 8 | 5 | 10 | 2 | 1 |
| *Euryopsis scriptipes* | 20 | 58 | 30 | 57 | 2 | 8 |
| *Enoplognatha ovata* | 0 | 3 | 1 | 3 | 0 | 1 |
| *Diponea tibialis* | 0 | 38 | 20 | 12 | 2 | 0 |
| *Diponea nigra* | 0 | 11 | 9 | 2 | 0 | 0 |
| *Dictyna completa* | 10 | 1 | 0 | 12 | 0 | 0 |
| *Dictyna idahoana* | 18 | 33 | 9 | 6 | 1 | 1 |
| *Metepeira foxi* | 27 | 85 | 50 | 73 | 12 | 11 |
| *Erigone dentosa* | 27 | 21 | 4 | 40 | 0 | 0 |
| *Spirembolus mundus* | 3 | 2 | 2 | 1 | 0 | 0 |
| *Frontinella communis* | 2 | 3 | 1 | 3 | 1 | 0 |
| *Araneus gemma* | 1 | 6 | 2 | 5 | 0 | 0 |
| *Araneus displicatus* | 1 | 4 | 1 | 4 | 0 | 1 |
| *Aculepeira verae* | 0 | 5 | 1 | 3 | 0 | 0 |
| Aranidae | 0 | 1 | 0 | 0 | 0 | 0 |
| Linyphidae | 0 | 0 | 0 | 3 | 0 | 0 |
| Unknown trapper | 0 | 4 | 6 | 3 | 2 | 1 |
| Trappers | 295 | 647 | 388 | 527 | 42 | 67 |
| Unknown | 93 | 4 | 3 | 1 | 0 | 0 |
| Total | 1421 | 3806 | 1312 | 2263 | 158 | 271 |

Table 2.—Results of the ANOVA of spider abundance on the experimental models.

| Source | df | SS | MS | *F* | *P* |
|---|---|---|---|---|---|
| Replicates | 4 | 1.210 | 0.303 | 0.45 | 0.7733 |
| Guild | 3 | 101.927 | 33.976 | 50.43 | 0.0001 |
| Height | 2 | 25.474 | 12.737 | 18.91 | 0.0001 |
| Orientation | 1 | 0.001 | 0.001 | 0.00 | 0.9666 |
| Guild × Height | 6 | 22.526 | 3.754 | 5.57 | 0.0001 |
| Guild × Orientation | 3 | 17.899 | 5.966 | 8.86 | 0.0001 |
| Height × Orientation | 2 | 4.617 | 2.308 | 3.43 | 0.0330 |
| Guild × Height × Orientation | 6 | 23.269 | 3.878 | 5.76 | 0.0001 |
| Error | 816 | 547.019 | 0.674 | | |

interaction was significant, and jumpers were most abundant on the 10 cm horizontal models (Fig. 4). This meant that there were unique combinations of height and orientation which had greater abundances of spiders from particular guilds. The most obvious interaction was that 70% of all pursuers were on the 0 cm vertical models. Jumpers were about equally abundant on all model types, but the effect of the interaction is evident when the abundances for the 10 cm models are compared. Jumpers were most abundant on the 10 cm horizontal models and least abundant on the 10 cm vertical models. Twenty-nine percent of all trappers were on 0 cm horizontal models.

## DISCUSSION

The spider community found on big sagebrush has a characteristic distribution of spider guilds that is dominated by jumpers (Ehmann 1994a; Abraham 1983). Previous studies suggested that plant architecture influenced guild abundance of spiders on big sagebrush (Ehmann 1994a; Wing 1984; Robinson 1981; Hatley & MacMahon 1980). In this study, the effects of two architectural variables on the distribution of spider guilds was tested using models that simulated the volume, branch texture and branch diameter of big sagebrush, while keeping the structural details simple enough to measure the two treatment variables (height above ground and branch orientation) and control for other variables. The models were placed among big sagebrush, so they were in the right habitat, and since spiders readily disperse (Dean & Sterling 1985; Bishop & Riechert 1990; Ehmann 1994b; Foelix 1996), they were in a habitat which contained a pool of potential colonists. Previous studies that examined habitat complexity, looked at the effect of single variables on the distribution of spiders. In this study, it was possible to test for the significance of the height by orientation interaction on the distribution of spider guilds. The significant three-way interaction indicated that branch orientation and height had a differential effect on guild abundance.

Table 3.—Total guild abundance for each model type over the two year (1997–1998) experiment using models to simulate shrub architecture. Numbers are the totals for seven sampling periods. Percentage of total abundance is in parentheses. 0 cm, 10 cm, and 40 cm = three height treatments. H = horizontal orientation and V = vertical.

| | 0 cm | | 10 cm | | 40 cm | | Guild |
|---|---|---|---|---|---|---|---|
| Guild | H | V | H | V | H | V | totals |
| Jumper | 44 (10.2) | 41 (9.5) | 54 (12.5) | 22 (5.1) | 31 (7.2) | 29 (6.7) | 221 (51.3) |
| Pursuer | 13 (3.0) | 58 (13.5) | 1 (0.2) | 7 (1.6) | 2 (0.5) | 2 (0.5) | 83 (19.3) |
| Ambusher | 2 (0.5) | 5 (1.2) | 3 (0.7) | 2 (0.5) | 5 (1.2) | 1 (0.2) | 18 (4.2) |
| Trapper | 32 (7.4) | 16 (3.7) | 15 (3.5) | 16 (3.7) | 11 (2.6) | 19 (4.4) | 109 (25.3) |
| Model totals | 91 (21.1) | 120 (27.8) | 73 (16.7) | 47 (10.9) | 49 (11.4) | 51 (11.8) | |
| Height totals | 211 (49.0) | | 120 (27.8) | | 100 (23.2) | | |

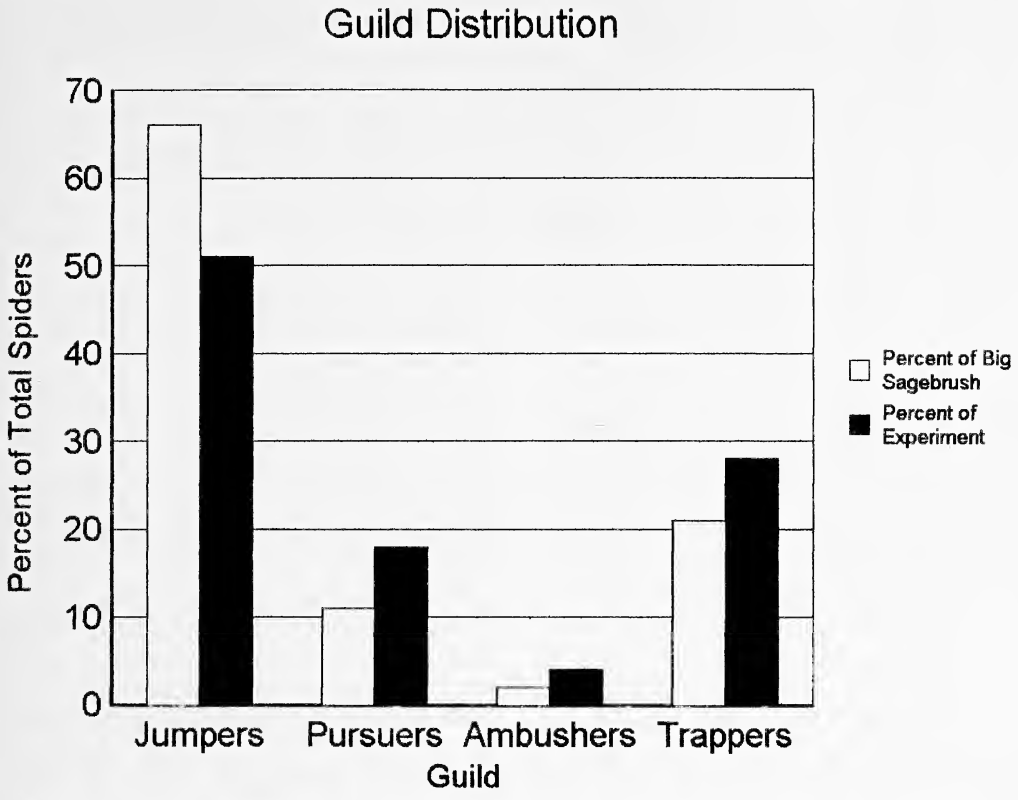


Figure 3.—Guild distribution of spiders from the Hyde Park census and from the experiment.

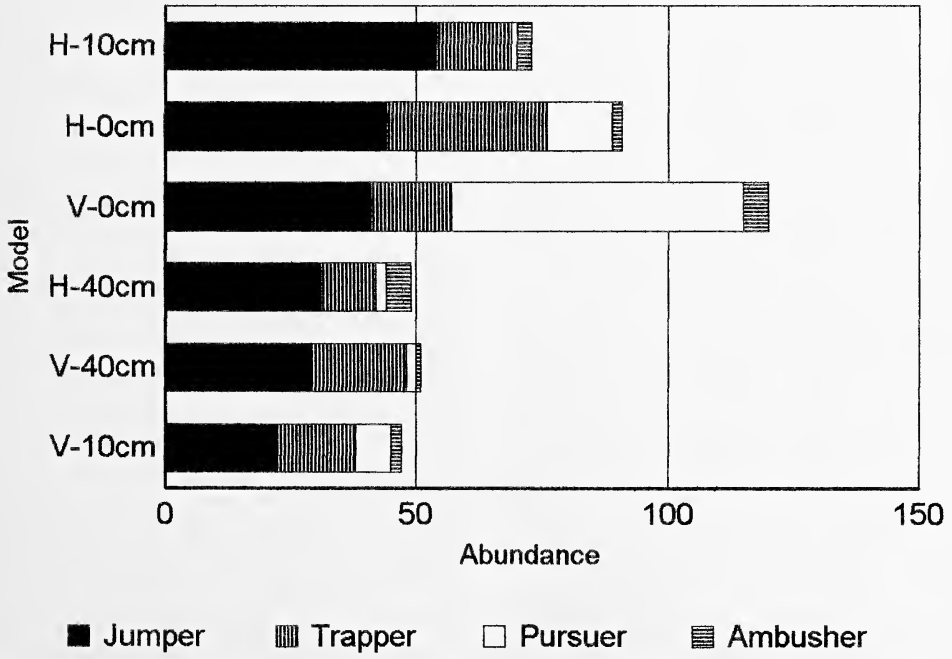


Figure 4.—Abundance of spiders by guild on models at two orientations (V = vertical and H = Horizontal) and three heights (0, 10, and 40 cm).

Seventy percent of all pursuers were found on the 0 cm, vertical models (Fig. 4). This model probably simulated grasses, and the most abundant pursuer in the experiment was *T. oblongus*, a grass specialist according to Roberts (1995), that is usually described as a sit-and-wait predator more like an ambusher than the other members of its guild (Gertsch 1979). The most common pursuer on big sagebrush at Hyde Park was *P. histrio*, but only one was collected from the models in the experiment.

Salticids and oxyopids are often more abundant on one vegetation type than another (Cutler et al. 1977; Abraham 1983). Jumpers are dominant on big sagebrush as they were on the horizontal models in the experiment. Jumpers were found in high numbers on all of the models, and there appears to be no differences between orientations on the 0 cm and 40 cm models. However, 71% of the jumpers on the 40 cm models were on those with horizontal orientations (Fig. 4). Sagebrush has significant horizontal components, so the horizontal nature of sagebrush may be one of the architectural variables to which jumpers are responding when they choose to remain on a shrub. The two-way interaction showed jumpers preferred horizontal models. In this experiment, jumpers were 51.4% of all spiders, which was within the range of jumpers found on big sagebrush in Hyde Park, but the most common jumper, *P. aeneola*, was virtually absent in the experiment. The decrease in numbers of *P. aeneola* was offset by higher numbers of *O. scalaris*. We do not know why there were species replacements. The important point is that there are redundant species and the guild distribution remained similar.

Salticids are among the most neurally sophisticated spiders (Forster 1982). The combination of a keen sense of sight, the ability to track prey even when the line-of-sight is interrupted and their unique jumping ability make them particularly adept at hunting in the structurally complex habitat found inside shrubs (Land 1969; Enders 1975; Jackson 1986; Jackson & Tarsitano 1993).

Jumpers may be using horizontality as a mechanism for recognizing that they are in a shrub, selecting habitat based on environmental cues (Orians & Wittenberg 1991). To understand these relationships additional studies are needed of the mechanisms responsible for these responses (Rypstra et al. 1999) and the life history and foraging behavior of these species (Neuvonen 1999).

The three-way interaction for trappers demonstrates a more complicated height by orientation interaction. Forty-four percent of all trappers were on the 0 cm models. Of those, two-thirds were on the horizontal models. This result agrees with Robinson's (1981) finding. A interesting feature of this three-way interaction is that an opposite result was found for the models placed 40-cm above the ground. Twenty-eight percent of all trappers were on these models, but, in this case, 63% of them were on the vertical models.

The distribution of orb-web weaving trappers and cob-web weaving trappers (using Abraham's (1983) designations) also differed between these two treatments, with a higher proportion of orb-weavers on the taller vertical models and a higher proportion of cob-weavers on the horizontal ground models. Perhaps placing all spiders that use webs as snares in the same guild is too simplistic. Uetz et al. (1999) recently divided trappers into more than one guild.

Ambushers play a minor role on big sagebrush, as was true in the experiment. Ambushers are sit-and-wait predators. Many sit in the flowers of plants waiting to ambush pollinators. The small flowers of big sagebrush do not provide good sites from which to ambush prey. The majority of ambushers on big sagebrush are probably using crevices in the bark as retreats.

The significant three-way interaction demonstrates that spider decision-making involves a complex integration of environmental cues. The models were purposely simplified so the two variables of interest could be experimentally manipulated. The simplification had the effect of eliminating other variables, which are characteristic of big sagebrush, that spiders may also use as cues in the decision-making process. Some of these variables are bark texture, leaf structure, color, phytochemicals, and structural complexity. The result from this experiment that two of the most prominent members of the Hyde Park big sagebrush spider community, *P. aeneola* and *P. histrio*, were virtually absent on the experimental models in both years, indicates that the decision-making process probably involves more than two variables.

The experimental nature of this study made it possible to establish the cause and effect relationship among the architectural variables and the distribution of spider guilds. Spiders use architectural cues as part of the decision-making process to establish residency on shrubs or to make an attempt at colonization elsewhere.

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# GROUP SIZE DOES NOT INFLUENCE GROWTH IN THE THERAPHOSID SPIDER *HYSTEROCRATES GIGAS* (ARANEAE, THERAPHOSIDAE, EUMENOPHORINAE)

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**ABSTRACT.** Spiderlings of the theraphosid spider *Hysterocrates gigas* were reared for 12 weeks with a superabundance of prey solitarily and in groups of two and four to examine the influence of rearing group size on growth. This taxon was selected because observations made on captive populations indicate that *Hysterocrates* spp. tarantulas have an unusually high level of mutual tolerance and captive juveniles have been observed to feed cooperatively on large prey until several months old. Cannibalism was only observed in one instance, in a group of four. There was no significant effect of rearing group size on increase in body mass. There was a tendency for a greater asymmetry in final weight in dyads than in tetrads. No difference was found in the amount of time spent feeding by individuals between the different group sizes. Hence, benefits of group living in *Hysterocrates gigas* spiderlings were not evident in this study.

**Keywords:** Tarantula, sociality, Mygalomorphae

Sociality in arachnids is a relatively rare phenomenon. Of approximately 36,000 described spider species, it is thought that only 35 are social; however, sociality has been demonstrated in at least 18 families of Araneae (Curtis & Carrel 1999). There are competing classification schemes for spider sociality (Aviles 1997), and the spectrum of spider sociality ranges from mutual tolerance to active cooperation in prey capture and brood care. One of the most significant thresholds along this continuum is the appearance of cohabitation by ecologically-competent juvenile spiders (i.e., those that could survive solitarily). These types of prolonged sibling aggregations are thought to represent an evolutionary step in the direction of quasisocial behavior in which sexually mature spiders exhibit cooperative behavior (Aviles 1997).

Sociality in spiders has presumably developed because of the benefits that come with direct cooperation and sharing the costs of silk production. Benefits of group living could include an increase in the amount and/or size of prey captured, shared construction costs of the web or increased predator avoidance (Aviles 1997; Uetz & Hieber 1997). Potential costs include direct competition for prey, increased predation or increased egg sac parasitism (Uetz & Hieber 1997).

Sociality has been widely studied in the araneomorph spiders, but has remained relatively unexamined in the mygalomorphs (Aviles 1997). Jantschke and Nentwig (2001) observed females of the subsocial diplurid spider *Ischnothele caudata* Ausserer 1875 caring for spiderlings by catching and sharing prey. The study by Darchen (1967) on the ischnocoline tarantula *Heterothele darcheni* (Benoit 1966) is the only documented case of sociality in theraphosids of which we are aware. Darchen found that these spiders display no aggression towards others in a group web, though they do not cooperate in hunting (Darchen 1967). Our study involved the theraphosid spider *Hysterocrates gigas* Pocock 1897. This West African tarantula lives in deep burrows in the rain forests and grasslands of Nigeria, Cameroon and the Congo (Smith 1990; Marshall 1996). *Hysterocrates gigas* burrows have been found in a wide variety of locations: at the base of trees, beneath rotted logs, in termite mounds, on roadside embankments, on the periphery of village compounds and on flat ground amongst palm groves, heavy grassland brush or dense tropical wet forests (Smith 1990; R. West pers. comm.).

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In this study we observed social interactions of *H. gigas* spiderlings in captivity. In captivity, we have observed this species sharing prey as juveniles up to several months of age. Although there have been no studies of *H. gigas* phenology in the wild, captive individuals may reach maturity in 18–24 months (S. Marshall pers. obs.). Observations in the field in Cameroon show that well-grown young will cohabit in the maternal burrow with the mother (R. West, pers. comm.). In an 11 week study conducted by Reichling & Gutzke (unpub. data), spiderlings of the closely-related *H. crassipes* Pocock 1897 swarmed together on a prey item subdued by the mother, which was then completely devoured. Reichling and Gutzke's observations demonstrate that sociality in *Hysterocrates* siblings can extend well beyond the first instar. In our study, sociality was observed for 12 weeks. We examined how group size (singles, dyads and tetrads) affected weight gain and feeding behavior in juvenile *H. gigas*. Because we had observed extended cohabitation of juveniles in captivity, as well as a unique group feeding behavior (i.e., cluster feeding) we predicted that *H. gigas* spiderlings reared communally would grow faster than those reared in isolation.

## METHODS

Test subjects were obtained from two different clutches of spiderlings produced by two wild-caught females collected in Cameroon and purchased from a commercial dealer (vouchers will be deposited at the American Museum of Natural History). The spiderlings remained in their communal sibling groups until we divided them into treatment groups. The treatment group sizes consisted of siblings placed as singletons, dyads or tetrads. The first clutch yielded seven replicates per group size and the second clutch yielded two replicates per group size. To differentiate individuals within groups, each spiderling (singletons included) was paint-marked on the dorsal side of the abdomen using Testors® enamel paint. At the beginning of the study, spiderlings from the two clutches differed in mass (Mean mg ± 1 SD: Clutch 1; 42.8 ± 14.2, $n = 49$, Clutch 2; 53.6 ± 18.7, $n = 14$). Because spiderlings within clutches were randomly assigned to treatment groups, this difference in starting mass was not associated with treatment group size (ANOVA on spiderling starting mass: Clutch, $F_{1, 57} = 8.82$, $P = 0.004$; Treatment Group Size, $F_{2, 57} = 1.74$, $P = 0.185$).

**Group Size and Weight Gain.**—Spiders were housed in translucent plastic 122 ml condiment containers in a 14 L: 10 D cycle. The room was kept at an average temperature of 26.6 °C (range: 23—31 °C) and average humidity of 44.1 % RH (range: 30–63%RH). Substratum was not provided in the rearing container in order to facilitate observation and collection of prey remains. The spiderlings were given approximately 2 ml of distilled water each week in the bottom of the container.

The spiderlings were fed once a week. Prey consisted of pre-killed (by freezing) crickets ranging in weight from 100–450 mg. All treatments received the same size class of cricket at each feeding. This cricket size insured that food would always be in overabundance, eliminating food competition between spiderlings. Pre-killed prey was offered so that very large prey items could be used, items too large for the spiderlings to subdue. In a pilot study it was determined that spiderlings would feed readily on pre-killed prey. Superabundance of prey was verified by the presence of uneaten prey remains, which were collected 24 hours after feeding.

Each spiderling was weighed to the nearest 0.1 mg in a tared plastic vial on an electronic balance before feeding and approximately 24 hours after feeding. The weights of the spiderlings were recorded for a period of 12 consecutive weeks. The average weekly weight gain was calculated within groups as was the coefficient of variation in weight gain for the last 4 weeks. Coefficients of variation are used to standardize variation in order to compare standard deviations of different sample sizes. A repeated measures ANOVA was used to assess the effect of group size on growth rates over the twelve weeks.

**Behavioral Mechanisms.**—Details of feeding behavior were observed from week 9 until the termination of the study at week 12. Behavioral observations were conducted to investigate any differences in time spent feeding between the spiders of the different sized treatment groups, any agonistic behaviors and occurrences of cluster feeding. Scan sampling was utilized to record the behavior of all spi-

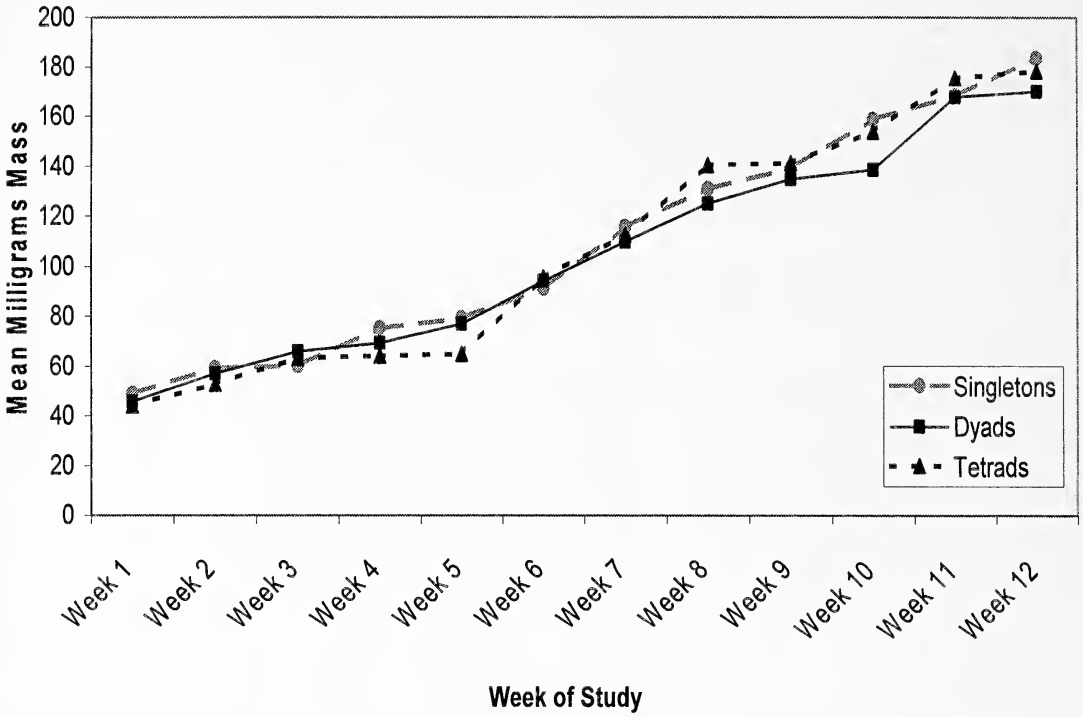


Figure 1.—Average weekly weight of *Hysterocrates gigas* spiderlings from two different maternal clutches in three treatment group sizes (singletons, dyads and tetrads).

derlings during feeding. The frozen prey was introduced into each rearing container in the afternoon (between 1400–1600 hours). Scan samples were taken once every hour from the introduction of prey until midnight. Spiderlings were observed under red light after dark, unless differentiating the color marks of the spiderlings was difficult, whereupon dim white illumination was used until the scan was complete.

The frequency of feeding behavior was compared across the different group sizes. To compare feeding behavior and weight gain, the proportion of hourly intervals during which feeding was observed was arc sine square root transformed to normalize the data. The transformed proportion of hourly intervals during which feeding was observed correlated with percent weight gain using a one-tailed Pearson's *r*. A repeated measures ANOVA was used to determine differences in amount of time spent feeding among treatment groups. For all statistics an alpha level of 0.05 was used.

## RESULTS

**Group Size and Weight Gain.**—For 12 weeks all groups of spiders gained weight at about the same rate. We found no significant effect of rearing group size on mass (repeated-measures ANOVA ; $F_{1,2} = 0.08$, $P = 0.925$). The average weekly weights showed no distinguishable trend in any one group (Fig. 1). The variability in weight gain as expressed by the coefficient of variation for the last four weeks also showed no discernable trend for any one group (Fig. 2).

**Behavioral Mechanisms.**—We observed the eight replicates of singletons, eight replicates of dyads and the five replicates of tetrads that remained at the end of the eighth week (unexplained mortality led to the loss of replicates during the course of the study). We recorded these behaviors: Investigating, Feeding, Antagonizing, Grooming and Cluster Feeding. Investigating was defined as the spiderling approaching the prey, contacting the cricket with the spiderling's front legs, but not commencing in consuming the prey item. Feeding was defined as the spiderling contacting the cricket with its mouthparts. Antagonizing was defined as: 1) chase, one spiderling chasing another spiderling around the container, 2) kick, kicking another spiderling

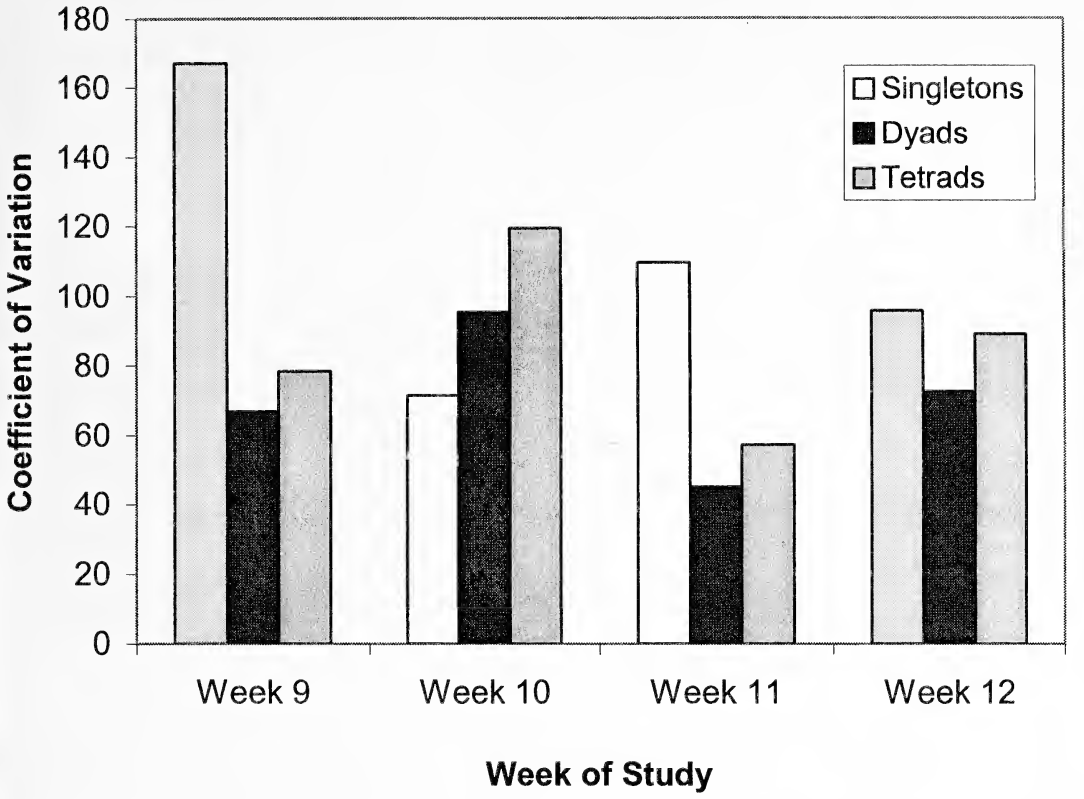


Figure 2.—Variability in weight gain in *Hysterocrates gigas* spiderlings for the final four weeks of the study. No difference in the coefficient of variation of percent weight gain was found between groups.

away from the cricket with its hind legs, or 3) take food, pulling the cricket away from the other spiderlings. Grooming was defined as a spiderling rubbing its legs together, over its abdomen, or over its cephalothorax. Cluster Feeding was defined as multiple spiderlings feeding on the same prey item at the same time, legs intertwined and no movement observed.

The most common feeding behavior we observed among tetrads was spiderlings feeding individually (Table 1). The next most common behavior was two spiders feeding at the same time, but not in contact with each other. Cluster feeding was only observed on 7 occasions (6.9% of observations). All occurrences of cluster feeding were observed in tetrads. Tetrads cluster-fed in groups of two, three or four.

We found a correlation between individual weight gain and the percent of observations

Table 1.—Feeding group sizes for *Hysterocrates gigas* spiderlings in tetrads. Tetrads were observed to feed in different sized groups. Number of occurrences lists number of hourly intervals.

| Feeding groups in tetrads | Number of groups in which incident was observed | Number of occurrences | Percentage of occurrences |
|---|---|---|---|
| One spider feeding | 5 | 79 | 77.5 |
| Two spiders feeding separately | 5 | 15 | 14.7 |
| Three spiders cluster feeding | 3 | 3 | 2.9 |
| Four spiders cluster feeding | 3 | 3 | 2.9 |
| Two spiders cluster feeding | 1 | 1 | 1.0 |
| Four spiders feeding separately | 1 | 1 | 1.0 |

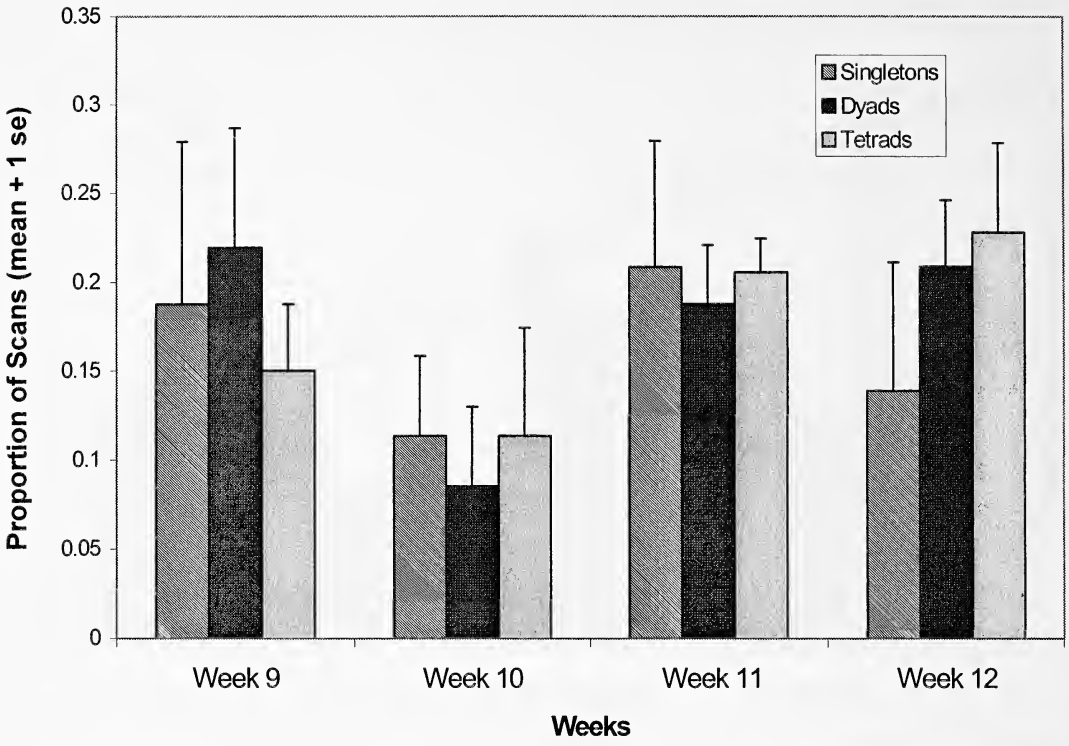


Figure 3.—Proportion of hourly intervals during which *Hysterocrates gigas* spiderlings were observed feeding by group size per week (mean +1 standard error).

during which an individual was observed feeding (Pearson's *r*: singletons, $n = 32$, $r = 0.488$, $P = 0.002$; dyads, $n = 64$, $r = 0.477$, $P < 0.001$; tetrads, $n = 80$, $r = 0.176$, $P = 0.059$). Using the Bonferroni adjustment for multiple correlations, an alpha level of 0.017 was set. For both the singles and the dyads, proportion of time spent feeding was significantly correlated with percent weight gain. No significant correlation was found in the tetrads.

We found that the proportion of time observed feeding was significantly different over the four weeks for the three treatment groups (repeated-measures ANOVA: $F_{1,3} = 3.077$, $P = 0.035$), showing that individual spiders differed each week in the amount of time they were observed feeding. However, the between-groups comparison indicated that the three treatment groups did not significantly differ from each other in proportion of time observed feeding ($F_{1,6} = 0.754$, $P = 0.609$) (Fig. 3).

A curious difference in mass was noted between individuals in dyads. Coefficients of variation of the spiderlings' final body weights at 12 weeks of age were used to compare the differences in spider size between dyads and tetrads. However, no significant difference was found between coefficients of variation of body mass of dyads and tetrads at week 12 ($t = 0.781$, df = 9, $P = 0.46$). We did find a significant positive correlation of coefficient of variation of final body weights and the number of aggressive incidents observed (Speaman's rho = 0.492, $P = 0.044$, $n = 13$).

## DISCUSSION

Over the 12 weeks of the experiment, spiders in each treatment group exhibited similar mass. We had anticipated a positive effect of group rearing based on the putatively adaptive cluster feeding behavior we observed because this feeding configuration appears to facilitate group feeding. So, why didn't we find a growth-related benefit associated with communal rearing conditions? It may be that the superabundance of food provided by design allowed all spiderlings to feed to satiation.

Krafft et al. (1986) demonstrated that conspecific tolerance in juveniles of *Coelotes terrestris* (Wider 1834) could be lengthened when there is an abundant supply of food. Similarly, Rypstra (1986) found that *Achaearanea tepidariorum* (C.L. Koch 1841), a solitary species, remained sociable longer when prey was abundant.

Small and large spiders in the dyads did not differ in the number of hourly scans observed feeding. However it was noted that the larger spider usually fed before its smaller counterpart if a large size discrepancy was present. Perhaps by feeding first the larger spider gained more nutritionally by feeding until satiation. This behavior could be seen as domination, but the smaller spider did feed later and for the same span of time. No difference was seen in the number of hourly intervals observed feeding within the individuals in tetrad groups. The most common feeding display in this treatment group was one spider feeding at a time.

As expected, weight gain correlated positively with hourly intervals observed feeding. Singletons, dyads, and tetrads were all observed feeding during the same number of hourly intervals. If there were some foraging advantage associated with feeding in groups, then individuals in groups of four should gain as much weight, or more, as individuals reared alone and spend less time feeding. Since this was not observed, there may be reasons (other than improved feeding efficiency) for social behavior to exist among young *H. gigas*. These benefits may include a reduced risk of predation, and the advantage of cooperatively seizing live prey.

Tetrads of *H. gigas* spiderlings in this study exhibited cluster feeding only 6.9% of the time. Cluster feeding is a communal feeding behavior that involves the spiders huddling with their legs intertwined. This is an unusual behavior that has been documented in *Aebutina binotata* Simon 1892, a communal cribellate spider (Aviles 1993). Adult *A. binotata* females captured and communally fed on large prey items such as cockroaches and beetles; juveniles fed when the adults left the prey (Aviles 1993). Jantschke and Nentwig (2001) observed spiderlings of the mygalomorph spider, *Ischnothele caudata* feeding together on a prey item provided by the mother, but there was no mention of the specific cluster feeding behavior such as we observed in *H. gigas*. *Ischnothele caudata* juveniles will also cooperate in catching larger prey for up to 18 weeks. Reichling and Gutzke (unpubl.) found *H. crassipes* spiderlings clustering around food items caught by the mother.

In our study there was only one instance of cannibalism in 18 groups: a spiderling in a tetrad killed its three siblings. Given the time span of the experiment and the number of group-reared *H. gigas* involved, we can tentatively conclude that cannibalism is rare in sibling groups of this species. The occurrences of agonistic behaviors in general may have been undercounted due to the use of scan sampling, because probabilities of recording temporally short displays of hostility or facilitation are low. Although agonistic behavior was observed, more lengthy focal observations might have better documented these interactions. Agonistic displays were similar in incidence in tetrads and dyads but did not occur in higher frequency as expected in tetrads, where more spiders were forced to interact. Aggression was not more readily observed between similarly-sized spiders, contrary to the group-living pholcid spider *Holocnemus pluchei* (Scopoli 1763) where fights over prey were most intense between spiders of comparable size (Jakob 1994). Instead, aggression was positively correlated with the coefficient of variation of final weights, showing that replicates containing spiders with large size discrepancies either engaged in more aggressive displays or aggression led to large size discrepancies. This concurs with findings on the social spider *Anelosimus eximius* in which larger females commandeer prey captured by smaller females (Ebert 1998).

*Hysterocrates gigas* spiderlings exhibited an unusual level of mutual tolerance, but this sociality did not apparently result in facilitation of feeding behavior, despite the distinctive cluster feeding posture we observed. Tarantulas, like all spiders, are generally cannibalistic beyond a short period of mutual toleration when young. *Hysterocrates* may be among the most sociable of theraphosid spiders. We have observed that *H. gigas* spiderlings in captivity will cohabit until several months of age. However, in a pilot study we conducted, *H. gigas* spiderlings that had been

first separated and then placed in social groups engaged in high levels of cannibalism, indicating that the suppression of cannibalism may depend on keeping the spiderlings in social groups after hatching. Cohabitation of sibling groups has been observed in at least three other mygalomorph spider taxa: *Nemesia cementaria* (Buchli 1969), *Heterothele darcheni* (Darchen 1967) and *Pamphobeteus* sp. Pocock 1901 (Cocroft & Hambler 1989). It remains to be seen how widespread this behavior is.

For social behavior to evolve organisms must have something to share, in the case of spiders this is a web or retreat, as well as an abundance of prey (Shear 1970; Rypstra 1993; Leborgne et al. 1998; Jantschke & Nentwig 2001). Contrary to Jantschke and Nentwig's (2001) claim that all social spiders must have a shared web for information transfer, very few mygalomorphs build webs. They construct burrows and in some cases the young will stay in the maternal burrow for extended periods of time (Buchli 1969). The burrow may promote sociality in the same way as a prey capture web. The increased level of sociality observed in this tarantula may result from the selective advantages accrued from sharing the deep maternal burrow and receiving protection from predators and harsh environmental conditions. *Hysterocrates* exhibits a high level of mutual tolerance and even unique feeding behaviors associated with prey sharing, making it an unexpectedly social tarantula. However, we have shown that group size does not influence the rate of growth.

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## SHORT COMMUNICATION

# A NEW SPECIES AND A NEW SYNONYMY IN THE SPINY ORB-WEAVER SPIDER GENUS *MICRATHENA* (ARANEAE, ARANEIDAE)

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**ABSTRACT.** A new species, *Micrathena cicuta*, is described and illustrated based on females from southeastern Brazil. *Plectana degeeri* Walckenaer is synonymized with *M. plana* (C.L. Koch), based upon the original description.

**Keywords:** *Micrathena*, Brazil, South America, systematics, new species

The genus *Micrathena* Sundevall 1833 is a common and conspicuous group of diurnal spiders endemic to the Americas. They can be easily recognized by their spiny abdomen, vertical orb-webs with an open hub and their characteristic upside down position on the webs, with the abdomen inclined horizontally. They differ from *Gasteracantha* Sundevall 1833 by the shape of carapace and from *Chaetacis* Simon 1895 by lacking spines or tubercles on the carapace behind the lateral eyes (Levi 1985). The genus was revised by Levi (1985) and comprises 104 species with a mostly Neotropical distribution. Of these, 33 are known only from females and except for two notes describing males of previously known species (Bonaldo 1990; Lise 1995) and the synonymy of *Thaumastobella mourei* Mello-Leitão 1945 with *Micrathena saccata* (C.L. Kock 1836) (Scharff 1991), the systematics of the genus has remained unaltered since Levi's revision.

In this paper we describe a new species, *Micrathena cicuta*, of the kirbyi group (as defined by Levi 1985). This is the largest species group in this genus and includes 45 species distributed from Central America to southern South America. Additionally, we synonymize *M. degeeri* (Walckenaer 1842) with *M. plana* (C.L. Koch 1836), another member of the kirbyi group, based upon the original description.

The specimens examined were deposited in the spider collection of the Instituto Butantan, São Paulo (IBSP) and Museu de Zoologia, Universidade de São Paulo (MZSP). The description format follows Levi (1985) and all measurements are in millimeters.

## RESULTS

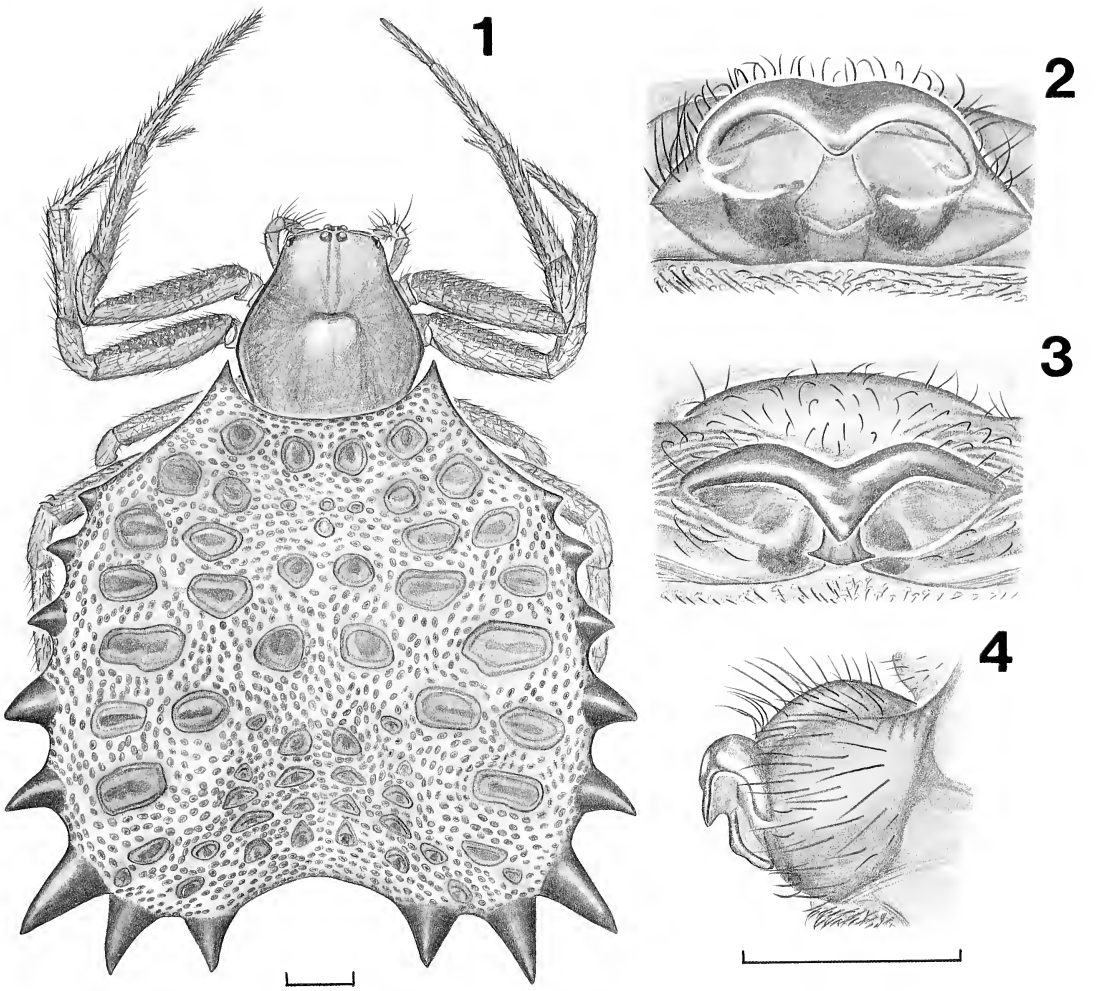
### *Micrathena cicuta* new species

Figs. 1–5

**Material examined.**—Holotype female, Volta Redonda, Área de Relevante Interesse Ecológico Floresta da Cicuta, 22°31′S 44°07′W, State of Rio de Janeiro, Brasil, 18 February 2002, M.O. Gonzaga (IBSP 36322). *Paratype*: 1 female, Resende, District of Serrinha do Alambari, 22°20′S 44°30′W, State of Rio de Janeiro, Brasil, E.F. Ramos, 31 March 1996 (IBSP 27195). *Other material examined*: BRASIL: *São Paulo*: Salesópolis, Estação Biológica de Boracéia, May 2001, equipe BIOTA, 1 ♀ (IBSP 39799); Cotia, Reserva Florestal de Morro Grande, 26 March 2003, A. A. Nogueira et al., 1 ♀ (IBSP 39794), 4 ♀ (IBSP, 39795–39798); 15 ♀ (MZSP).

**Etymology.**—The specific name is a noun in apposition taken from the type locality.

**Diagnosis.**—*Micrathena cicuta* shares with *Micrathena clypeata* (Walckenaer 1805) a flat abdomen with rounded sides, covered by several sclerotized disks and minute granules and with one anterior pair of spines. It is distinguished by the abdomen with 8 marginal pairs of black thorns (5 in *M. clypeata*) and by the absence of dimples on the carapace (Fig. 1). The epigynum differs by the narrower lateral lobes and median plate in ventral




Figures 1–4.—*Micrathena cicuta* new species. 1. Female habitus, dorsal view. 2. Female epigynum, posterior view. 3. Ventral. 4. Lateral. Scale bars, 1 = 1.00 mm; 2–4 = 0.50 mm.

and posterior views (Figs. 2, 3), the anteriorly notched transverse bar with a longer and posteriorly directed lobe (Fig. 3) and by the rounded bulge in lateral view (Fig. 4).

**Description.**—Male: Unknown.

*Female (holotype):* Carapace orange, with a high thoracic region. Clypeus, chelicerae, labium, endites and sternum orange. Palpus and legs orange-brown, darker ventrally. Abdomen orange, lighter than carapace, with one anterior pair of spines overhanging carapace and 8 pairs of marginal black thorns. Dorsum of abdomen flat with a slight posterior median longitudinal depression. Dorsal sclerotized disks and minute granules as in *M. clypeata*. Total length 8.6, carapace 2.8 long, 2.5 wide. First femur 2.3; patella and tibia 2.5; metatarsus 1.0; tarsus 0.6. Second patella and tibia 2.3; third patella and tibia 1.4. Fourth femur 3.2; patella and tibia 2.3; metatarsus 1.6; tarsus 0.7.

**Distribution.**—Known only from southeastern Brazil. This species seems to be closely related to *M. clypeata*, which occurs in Panama, northern South America and the Amazon Basin (Fig. 5). These two species display a disjunct distribution, occurring in tropical rainforest areas separated by central and northeastern Brazilian savanna vegetations (cerrado and caatinga, Hueck 1972).

### *Micrathena plana* (C.L. Koch)

*Acrosoma planum* C.L. Koch 1836:81, fig. 228.

*Micrathena plana*: Levi 1985:509, figs. 311–325, map 6.

*Plectana degeeri* Walckenaer 1842:174 (female holotype from Suriname, lost) NEW SYNONYMY.

*Acrosoma degeeri*: Butler 1873:425.

*Micrathena degeeri*: Petrunkevitch 1911: 368; Platnick 2003.

**Remarks.**—*Micrathena degeeri* was overlooked


Figure 5.—Geographic distribution of *Micrathena clypeata* (gray area, based on records from Levi 1985) and locality records for *Micrathena cicuta* new species (circles).

by Levi (1985), and the type specimens are lost like so many of the species described by Walckenaer (1842). According to the original description (Walckenaer 1842:174), *M. degeeri* possesses an oval-triangular abdomen with 12 spines: an anterior pair of small ones (described as "médiocre" by the author), a pair of large and diverging posterior spines with two small ones on the base, one dorsal and one ventral. The sides of the abdomen were described as bearing two small spines. This description matches Levi's (1985) illustrations of *Micrathena plana*, a species distributed from Panama and the West Indies to Argentina, and the only species with 12 abdominal spines recorded from Suriname. As such, we here consider *M. degeeri* a junior synonym of *M. plana*.

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## SHORT COMMUNICATION

# COLOR DIMORPHISM IN ADULTS AND JUVENILES OF *BUITINGA SAFURA* (ARANEAE, PHOLCIDAE)

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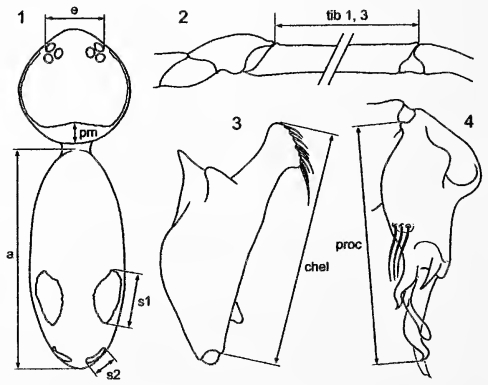
**ABSTRACT.** We document the first case of a color dimorphism in a pholcid spider. Males, females and juveniles of *Buitinga safura* Huber 2003 either have large black spots on the abdomen or no spots, with no intermediates. At the same time, this species shows sexual dimorphism (brown prosomal marks present in males only) and continuous prosomal pattern variation in males, females and juveniles. The abdominal pigment is located in the hypodermis.

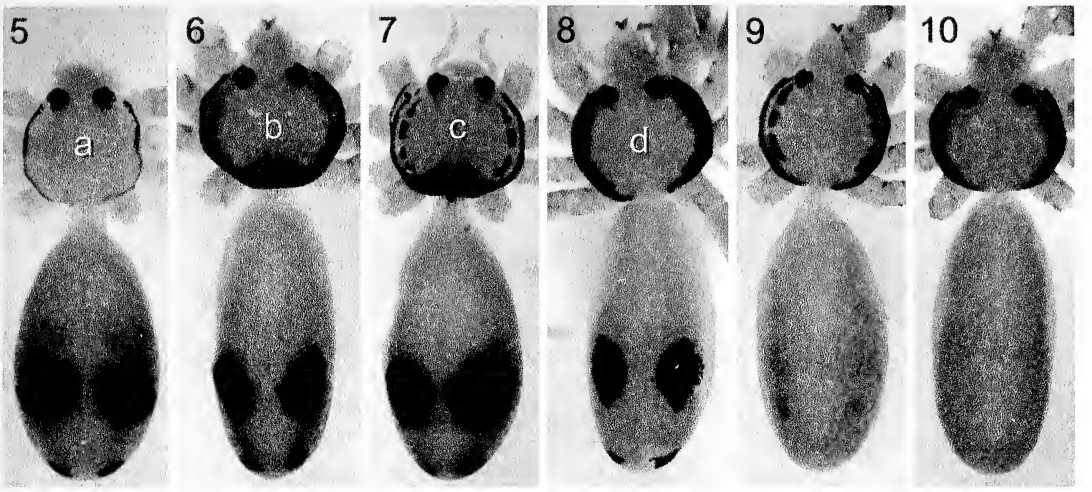
**Keywords:** Color dimorphism, polymorphism, pattern variation, Pholcidae

Intrasexual polymorphism (discontinuous individual variation among members of the same sex, in the same life stage, within a population) is considered a key phenomenon for the study of basic evolutionary concepts (e.g., West-Eberhard 1989; Gould 1989; Eberhard & Gutierrez 1991; Mayr & Ashlock 1991; Emlen 1994). Color polymorphisms, being easily visible, are among the best studied and considerable progress has been made introducing spiders as possible model arthropods with which to study the evolutionary processes working on visible, intraspecific variation. Spectacular examples include the candy-striped spider, *Enoplognatha ovata* (Clerck), and the Hawaiian happy-face spider, *Theridion grallator* Simon, but many cases have been described in various spider families. Extensive reviews on spider coloration and polymorphism have been published recently by Oxford & Gillespie (1998) and Oxford (1999).

We present here the first case of a color polymorphism in the spider family Pholcidae. A large series of *Buitinga safura* Huber 2003 was collected in the Uzungwa Mountains, Iringa Province, Tanzania (for details of study site, see Sørensen et al. 2002), by an expedition of the Smithsonian Institution in Washington, D.C. and the Zoological Museum of Copenhagen in May 1997. The material studied herein is deposited in the National Museum of Natural History (Washington, D.C., U.S.A.). Specimens were collected from litter and logs, low vegetation, understory and canopy, and transferred to 70% ethanol (Sørensen et al. 2002). The present analysis is restricted to the largest subsample, i.e. to the 1139 specimens collected from the understory, but inspection of the other material suggests that the patterns described below do not differ significantly among habitats. We measured nine traits (Figs. 1–4) with a measuring grid in the ocular of a Nikon SMZ-U dissecting microscope and assessed prosomal pattern variation in a qualitative way (Figs. 5–8). Tables 1 and 2 give the sample sizes, means, ranges, standard deviations, coefficients of variation, significance values of Kolmogorov-Smirnov tests for normal distribution and estimates of measurement error for all measured traits.




Figures 1–4.—Illustrations of characters measured. 1. Prosoma and abdomen, dorsal view; a = abdomen length, e = eye distance, pm = posterior mark on carapace, s1, s2 = abdominal spot 1 and 2 lengths. 2. Tibia, lateral view; tib 1,3 = tibia 1 and tibia 3 lengths. 3. Right male chelicera, lateral view; chel: chelicera length. 4. Left procursus, prolateral view; proc = procursus length.




Figures 5–10.—Photographs of six adult *Buitinga safura* specimens showing some of the color variation described: abdominal spots present (5–8) vs. absent (9–10), posterior mark on carapace present (6–7) vs. absent (5, 8–10), brown bands on carapace present (6, 8, 10) vs. absent (5, 7, 9), and the four arbitrarily defined degrees of lateral prosomal patterns: a (only black lines), b (black lines plus brown bands), c (black lines plus three pairs of black spots), d (black lines plus brown bands plus three pairs of black spots).

From 341 adult males in the sample, 20 had two pairs of spots on the abdomen, two had only one (the posterior) pair of spots. These 22 spotted males were all measured. From the remaining 319 spotless males, 23 were randomly selected and included in the quantitative analysis, resulting in a total of 45 males measured. Histograms of male spot lengths clearly indicate that these are not cases of continuous variation (Figs. 11, 12). All other traits measured (with the exception of the posterior mark on the carapace, see below) show unimodal distributions that are not significantly different from normal distributions (Table 1). All specimens are considered conspecific because those characters that in pholcids differ most among species (procursus, bulb, cheliceral armature; see Huber 2003) were virtually identical. From a scatter between two characters with high interspecific variation (procursus, chelicerae), it is evident that spotted (o) and spotless (+) males occur at any sizes of these characters (Fig. 13). Also, there was no correlation between overall size and abdominal pattern (Fig. 14; t-test calculated for tibia 1 length, tibia 3 length, and eye distance: all $P > 0.05$). Ordinary least squares (OLS) regressions of log-transformed characters were calculated for all traits on eye distance as an indicator of body size (for justification of method see Eberhard et al. 1999). As in the comparative study by Eberhard et al. (1998), legs and other non-genitalia had relatively high slopes (tibia 1 length

Table 1.—Male characters measured, with sample sizes ($n$), means, ranges, standard deviations (SD), coefficients of variation (CV), significance values of Kolmogorov-Smirnov tests for normal distribution (KS), and estimates on measurement error.

| Character | $n$ | Mean (mm) | Range (mm) | SD | CV | KS | Measurement error (± mm) |
|---|---|---|---|---|---|---|---|
| Tibia 1 length | 39 | 5.65 | 5.00–6.13 | 0.286 | 5.1 | 0.81 | 0.07 |
| Tibia 3 length | 44 | 2.48 | 2.20–2.73 | 0.109 | 4.4 | 0.47 | 0.03 |
| Abdomen length | 45 | 1.90 | 1.58–2.25 | 0.166 | 8.7 | 0.24 | 0.03 |
| Eye distance | 44 | 0.56 | 0.52–0.60 | 0.018 | 3.2 | 0.21 | 0.01 |
| Chelicera length | 44 | 0.60 | 0.53–0.63 | 0.024 | 4.2 | 0.62 | 0.01 |
| Procursus length | 43 | 0.53 | 0.51–0.56 | 0.012 | 2.4 | 0.48 | 0.01 |
| Abdominal spot 1 | 20 | 0.48 | 0.38–0.60 | 0.061 | 12.7 | 0.00 | 0.03 |
| Abdominal spot 2 | 22 | 0.24 | 0.15–0.35 | 0.042 | 17.4 | 0.00 | 0.03 |
| Carapace posterior mark | 7 | 0.26 | 0.05–0.38 | 0.117 | 44.3 | 0.00 | 0.03 |

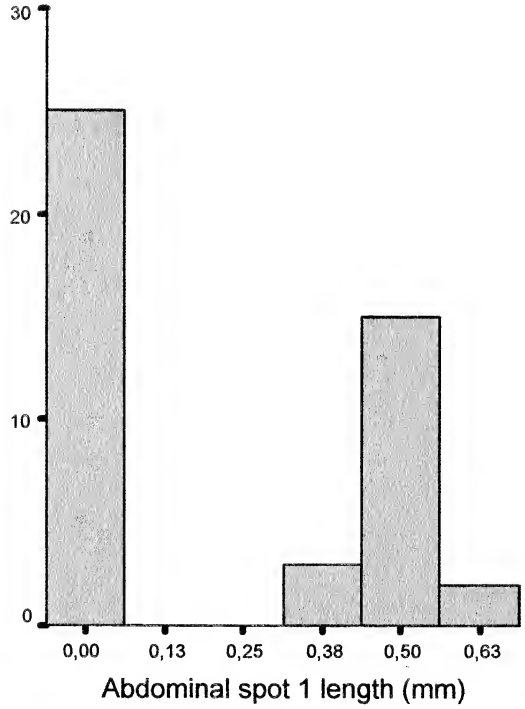
Table 2.—Female characters measured, with sample sizes ($n$), means, ranges, standard deviations (SD), coefficients of variation (CV), significance values of Kolmogorov-Smirnov tests for normal distribution (KS), and estimates on measurement error.

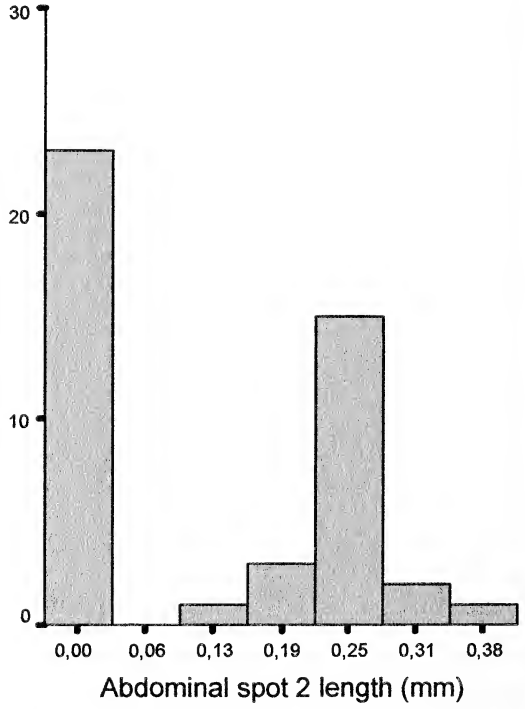
| Character | $n$ | Mean (mm) | Range (mm) | SD | CV | KS | Measurement error (± mm) |
|---|---|---|---|---|---|---|---|
| Tibia 1 length | 50 | 4.75 | 4.37–5.23 | 0.196 | 4.1 | 0.70 | 0.07 |
| Tibia 3 length | 54 | 1.98 | 1.87–2.17 | 0.070 | 3.5 | 0.19 | 0.03 |
| Abdomen length | 56 | 1.75 | 1.38–2.18 | 0.157 | 9.0 | 0.87 | 0.03 |
| Abdominal spot 1 | 29 | 0.49 | 0.35–0.73 | 0.084 | 17.3 | 0.00 | 0.03 |
| Abdominal spot 2 | 31 | 0.21 | 0.13–0.28 | 0.037 | 17.7 | 0.00 | 0.03 |
| Carapace posterior mark | 4 | 0.20 | 0.13–0.28 | 0.061 | 30.6 | 0.00 | 0.03 |

= 1.00; tibia 3 length = 0.79; chelicerae length = 0.73; all $P < 0.001$), while procursus length had a much lower slope (0.38; $P < 0.001$), as is usual for genitalia. This trend remained when spotted and unspotted individuals were analyzed separately, but there was considerable variation among slopes of spotted vs. unspotted males (probably due to small sizes of subsamples). The slope of abdomen length on eye distance was non-significant.

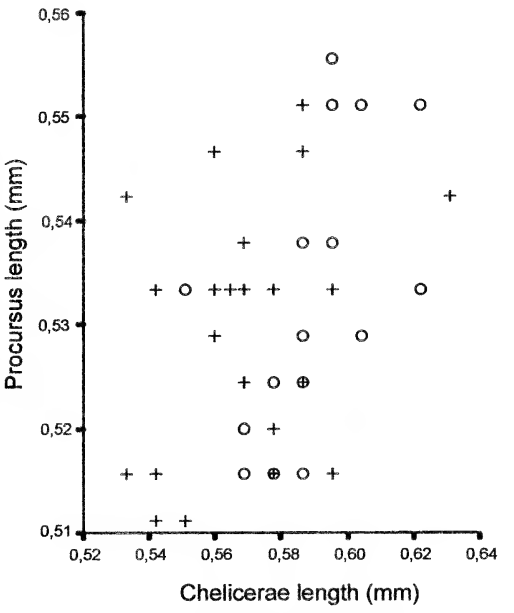
Male prosomal pattern variation was also substantial. However, this variation was continuous and not dimorphic. We arbitrarily defined four types within the continuum of lateral prosomal patterns (Figs. 5–8), but found no significant correlation of these with body size (Fig. 15) or abdominal pattern (Fig. 16). In seven (out of 341) males, there was a large black mark posteriorly on the carapace (Fig. 6). This trait may be dimorphic too, but sample size is obviously too small. All of these males also had abdominal spots, but two of them had only the posterior pair.

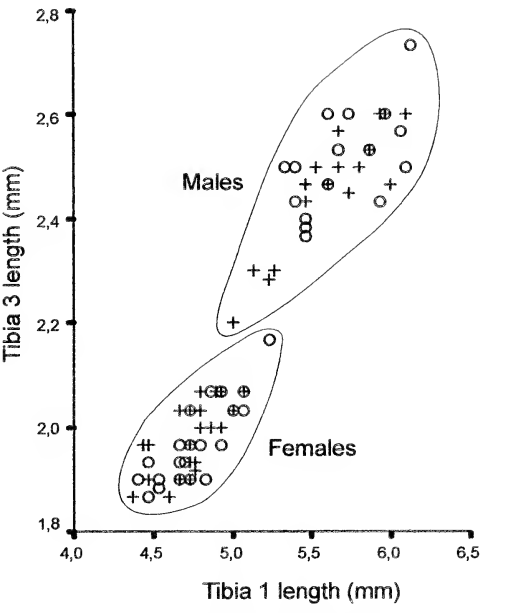
In females we measured the same traits except for eye distance, procursus length and chelicera length. From the 385 adult females in the sample, 29 had both pairs of abdominal spots, two had only one (the posterior) pair, all others were spotless.



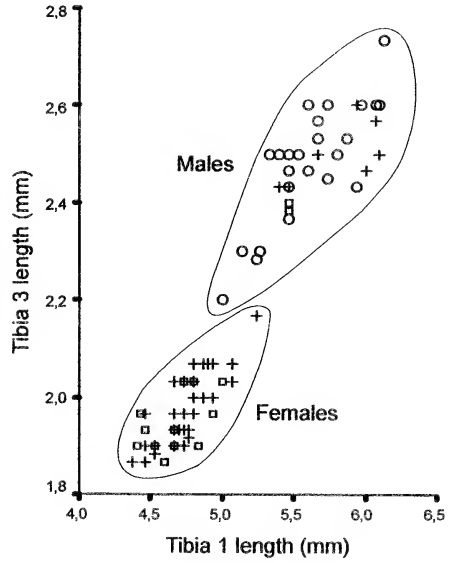



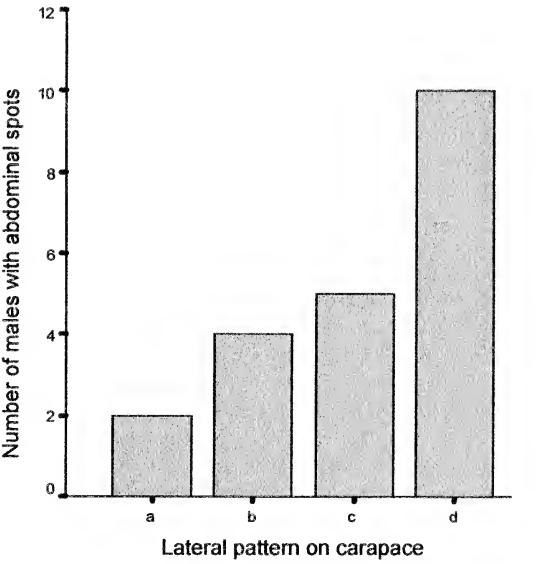

Figures 11, 12.—Histograms showing the bimodal distributions of abdominal spot sizes in males. Note that the left bars indicating spotless specimens represent only a small fraction of the more than 300 spotless males in the original sample.




Figures 13, 14.—Scatter diagrams showing the presence or absence of abdominal spots (o = spotted, + = spotless) in males with different sizes of chelicerae and procursi (13) and in males and females of different overall size as indicated by leg length (14). Fig. 13 strongly supports conspecificity of spotted and spotless males, while Fig. 14 shows that there is no correlation between abdominal spottedness and size.




Figures 15, 16.—15. Scatter diagram showing the distribution of lateral prosomal patterns in males and females of different sizes: pattern "a" (Fig. 5; represented by squares) occurs in males and females but is rare in males; patterns "b" and "d" (Figs. 6 and 8; represented by circles) occur only in males; pattern "c" (Fig. 7; represented by crosses) occurs in both sexes. 16. Bar diagram showing that abdominal spots occur in males with all different kinds of prosomal patterns. Sample size is too small to judge the significance of the increase in cases of abdominal spots from a–d.

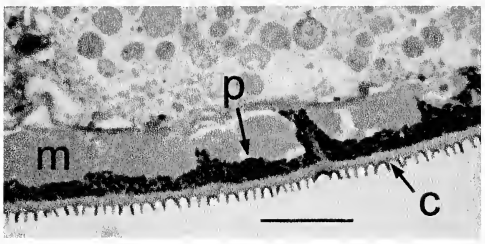



Figure 17.—Semithin section of a female abdomen in the area of a spot, showing the location of the pigment in the hypodermis; c = cuticle, m = subcuticular muscle layer, p = pigment. Scale line: 25μm.

From these, 25 randomly chosen individuals were measured resulting in a total of 56 measured females. Abdominal spot sizes in females were similar to those in males (see Tables 1 and 2) and the proportions of spotted vs. unspotted specimens was not significantly different in males vs. females (chi square = 0.684, $P = 0.408$, 1 df). However, females never had brown marks on the prosoma, i.e. they showed only two of the four lateral prosomal patterns shown in Figs. 5–8. Therefore, in addition to the abdominal intrasexual dimorphism there is also an (inter)sexual dimorphism. Posterior black marks occurred in four females and all of these also had abdominal spots, but two of them only the posterior pair. The epigyna of all females were indistinguishable.

In juveniles we only counted the numbers of spotted and spotless specimens (19 vs. 394). The percentage of spotted individuals was similar to that in adults (chi square = 4.022, $P = 0.134$, 1 df). Most juveniles were late or penultimate instars. Prosomal pattern variation in juveniles appeared similar to that in females, but most juveniles had only the black lines (cf. Fig. 5) and lateral spots, if present, were usually very weak. Posterior black marks on the carapace were not seen in juveniles.

The abdominal pigment is located in the hypodermis: removal of the digestive tract left the spots intact, but after treatment with NaOH they could be removed easily from the cuticle using a brush. This result was confirmed by preparation of semithin sections (Fig. 17). By comparison with other spider pigments (Oxford & Gillespie 1998), the location suggests it is an ommochrome. There is no evidence that preservation in ethanol has had any effect on the abdominal spots: they are either deep black or entirely absent. Little can be said beyond these basic facts. The truly interesting questions remain to be answered: is the polymorphism genetically determined? Is it selectively maintained, and if yes, by which selective forces? What are the costs of producing spots, if any? How many alleles contribute to the polymorphism, and which morph is dominant?

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## SHORT COMMUNICATION

# *PARDOSA MILVINA* (ARANEAE, LYCOSIDAE) SPIDERLING MOVEMENT IN THE PRESENCE OF CONSPECIFIC AND HETEROSPECIFIC SILK AND EXCRETA

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**ABSTRACT.** Adult females of the wolf spider *Pardosa milvina* (Hentz 1844) are known to show adaptive antipredator responses in the presence of chemical cues (silk and excreta) from the larger co-occurring wolf spider *Hogna helluo* (Walckenaer 1837). We tested if the presence of *H. helluo* cues affected *P. milvina* spiderling dismounts from their mothers. Immediately after females opened their egg sacs, we counted offspring and placed spiderling-carrying females on one of three experimental substrates: 1) container previously occupied for 24 h by an adult conspecific female, 2) container previously occupied for 24 h by a juvenile *H. helluo* equal in mass to an adult *P. milvina*, or 3) a control container devoid of either cue. We then measured the proportion of spiderlings that dismounted from their mothers over a six-day period. Spiderling dismounts peaked by day three, after which spiderlings tended to return to their mother. During day one, significantly fewer spiderlings were dismounted from the mother in containers previously occupied by a juvenile *H. helluo* compared to other treatments. There was no significant difference in dismounts among treatments during days 2–6. Since spiderlings were maximally dismounted by day three, we suggest that spiderlings may tend to disperse into areas with fewer *H. helluo*.

**Keywords:** Spiderlings, lycosid, dispersal, chemical cue, *Hogna helluo*

The wolf spider *Pardosa milvina* (Hentz 1844) and its larger intraguild predator, *Hogna helluo* (Walckenaer 1837) are common throughout agricultural systems in the Midwestern United States (Marshall & Rypstra 1999). Recent studies show that predator-prey interactions among these species are mediated in part through each other's silk draglines and excreta (Persons & Rypstra 2000; Persons et al. 2001). Adult female *P. milvina* respond to chemical cues (silk and excreta) from adult and juvenile *H. helluo* with a suite of antipredator behaviors including substratum avoidance, reduced activity and vertical movement (Persons et al. 2001, 2002; Persons & Rypstra 2001). In contrast, adult female *P. milvina* are unresponsive to conspecific female silk and excreta (Persons et al. 2001, 2002).

Female wolf spiders typically carry their egg sac by attaching it to their spinnerets for a period of several days to more than two months and after opening the egg sac, continue to transport spiderlings on their dorsum for a period of several days to a week or more (Fujii 1976). Spiderlings then disperse primarily via asynchronous dismounting from their mother as she moves through the environment (Fujii 1976) and secondarily via aerial dispersal (Glick 1939; Richter 1970). Juveniles may also periodically dismount and remount their mothers prior to permanent dispersal to drink or reposition themselves for more efficient transport (Eason 1964; Higashi & Rovner 1975).

*Pardosa milvina* spiderlings may benefit substantially by dismounting their mother when in microhabitats that are devoid of *H. helluo* and their associated chemical cues. Although predator-induced reductions in activity increase survival of *P. milvina* when in the presence of a live *H. helluo* (Persons et al. 2001, 2002; Barnes et al. 2002), these defensive behaviors are costly and contribute to reduced foraging and reproductive success (Persons et al. 2002). Also, under some circumstances, *H. helluo* are attracted to substrates previously occupied by adult female *P. milvina* (Persons & Rypstra 2000) which may further increase predation risk to *P. milvina* spiderlings. Here we tested if the presence of silk and excreta from juvenile *H. helluo* significantly affected the timing of juvenile *P. milvina* dismounts from their mothers.

Sixty-eight mated adult female *P. milvina* were field caught in late May and early June, 2000 within soybean fields on Susquehanna University property adjacent to campus (Selinsgrove, Snyder County, Pennsylvania). All field-collected females were either carrying egg sacs or produced them shortly after being caught. Spiders were individually main-

tained with their egg sacs in white plastic containers with transparent lids (9 cm d, 7 cm h). A small vial lid was placed on the bottom of the container with a few drops of water to serve as a source of moisture and humidity. All spiders were kept at room temperature (23—25 °C) with a 13L:11D photoperiod. Females were given constant access to fruit flies (*Drosophila melanogaster* (Meigen 1830) as a food source and checked daily for spiderling emergence from the egg sac. Because filial or sibling cannibalism is possible among lycosids, we chose to count spiderlings immediately after egg sac emergence to insure an accurate measure of clutch size. After emergence, spiderlings were gently removed from the mother with a soft-bristled paintbrush, counted, and allowed to climb back on their mother. The females with offspring were then randomly assigned to one of three substrate treatments: 1) a container that previously held a juvenile *H. helluo* for 24 h that was equal in mass to an adult female *P. milvina* ($n$ = 25); 2) a container that previously held an adult conspecific female *P. milvina* (without an egg sac), ($n$ = 22) for 24 h; or, 3) a blank control container devoid of either cue ($n$ = 21). *Pardosa milvina* and *H. helluo* used for generating chemical cues were maintained on an ad libitum diet of fruit flies (*D. melanogaster*) prior to being placed in their respective treatment containers. *Hogna helluo* and *P. milvina* were not fed during the time they were used to deposit silk and excreta nor were test *P. milvina* allowed to feed during the trial period. The deposited silk and excreta used as test substrates was not renewed for the duration of the experiment. Female test spiders were initially checked 24 h after being placed on their respective substrate treatments and again every 24 h afterwards for six consecutive days. All *P. milvina* with spiderlings were provided with a small inverted vial cap filled with water during the entire test period. The total number and proportion of spiderlings that had dismounted from their mother was recorded for each replicate. Only a spiderling that had no direct physical contact with its mother was considered dismounted.

Egg sac clutch sizes of *P. milvina* for all treatments varied between 1–101 spiderlings (mean = 31.8 ± S.E. 2.18 offspring; median = 30.5 offspring). Therefore we used the proportion of dismounted spiderlings/egg sac as the dependent variable in our analysis. We angular transformed our proportions to conform to assumptions of normality and performed a repeated-measures two-way ANOVA with chemical cue treatment (fixed effect) and day (random effect) as factors (as in Sih & McCarthy 2002).

Peak spiderling dismounts occurred three days post-emergence (mean 78.3% for all treatments combined)(Fig. 1). By day six of post-emergence, the mean proportion of dismounted spiderlings returned to similar levels observed during the first day. Substrate type had a significant effect on spiderling dismounts ($F_{2,65}$ = 3.69; $P$ = 0.0301). There was also a significant day effect ($F_{5,65}$ = 22.22; $P$ < 0.0001). However, there was no significant day by treatment interaction ($F_{5,2}$ = 1.22; $P$ = 0.276). To better understand dismounting patterns across chemical cue treatments but within days, we performed six *a posteriori* multiple comparison tests (Tukey test for unequal sample sizes) for ANOVAs as described by Zar (1984).

Based on the results of the Tukey tests, significant substrate effects were attributable solely to differences in spiderling dismounts during the first day of emergence. Females placed in containers with *H. helluo* chemical cues had an average of only 28% (mean 8.76 ± S.E. 2.36 spiderlings) of their clutch dismounted by day one compared to 41% (mean 13.23 ± S.E. 3.20 spiderlings) and 55% (13.71 ± S.E. 2.44 spiderlings) for the *P. milvina* and control treatments respectively. During the first day of emergence, a significantly lower proportion of spiderlings dismounted in the *H. helluo* cue treatment than either the *P. milvina* treatment or blank control. However, the blank control and *P. milvina* treatments were not significantly different from each other. Proportion of spiderling dismounts among treatments for all other days was not statistically significantly different based on Tukey post-hoc comparisons.

Other studies of spiderling dispersal times among *Pardosa* species have found ranges of 2–7 days for *P. milvina* (Montgomery 1903), 4–8 days for *P. laura* (Karsch, 1879)(Fujii 1976), and 3–7 days for *P. t-insignita* (Bösenberg & Strand 1906)(Fujii 1976). None of these studies noted remounting behavior among spiderlings but dismounting and remounting for purposes of water seeking are known to occur among lycosids (Higashi & Rovner 1975). Since spiderlings were not marked, it was not possible to determine the frequency of remounting by individual spiders. We noted that mounted spiderlings would frequently crawl down one of the mother's legs and lightly tap at the ground. Afterwards they would either climb back onto the mother's dorsum, or dismount entirely. This behavior suggests a mechanism by which spiderlings may sample the substratum directly prior to dismounting. We also noted that dismounted spiderlings tended to remount their mother only after direct physical contact rather than showing directional orientation and approach toward the mother from other parts of the container. These observations indicate that remounting tends to be incidental with further maternal contact rather than a directed response from the spiderling at a distance.

The differences in spiderling dismounts between treatments were modest, yet there was a significantly smaller proportion dismounted from their

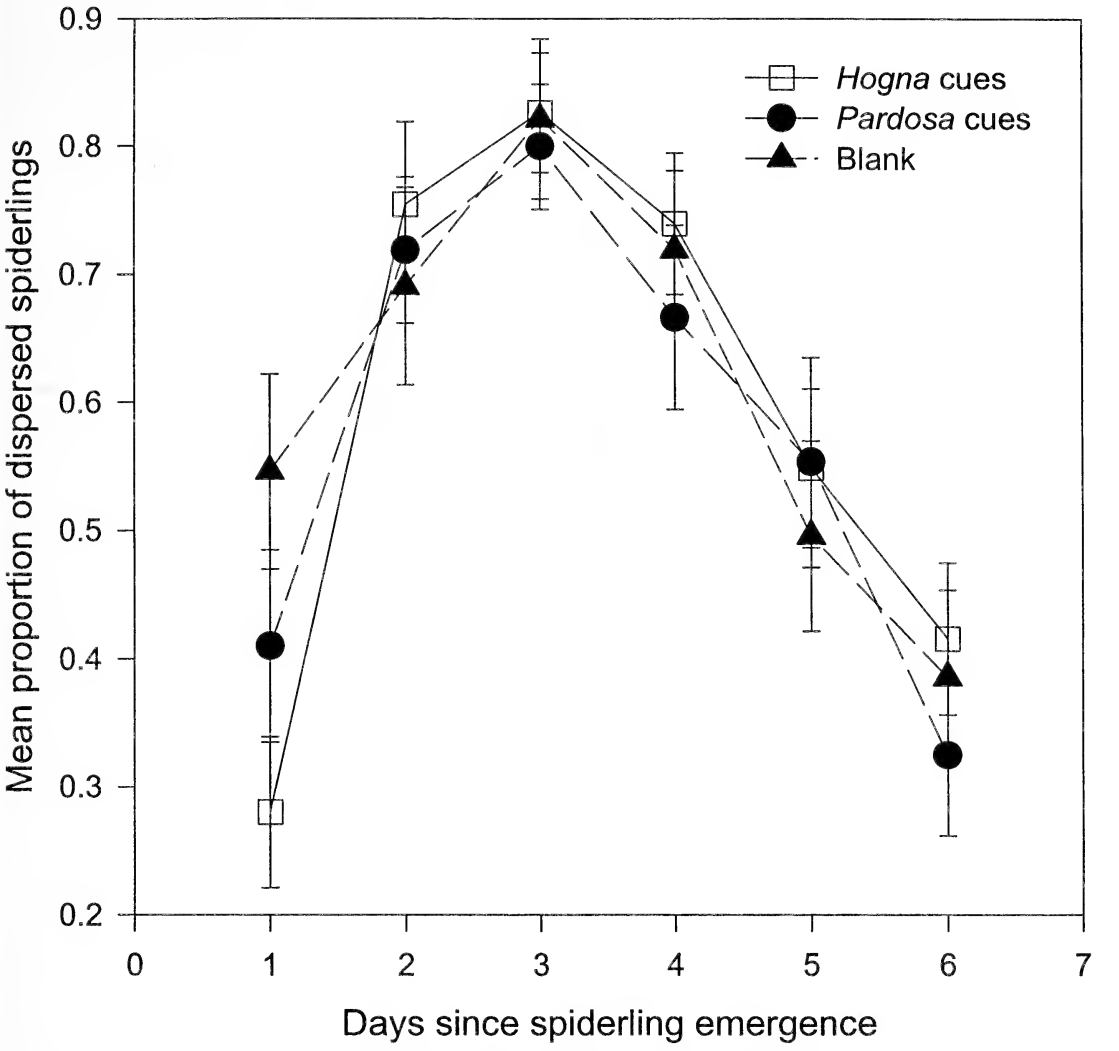


Figure.—Mean proportion of spiderlings dispersed from their mothers (± S.D.) while on substrates previously occupied by a conspecific female *P. milvina* for 24 h (*Pardosa* cues), a juvenile *H. helluo* (*Hogna* cues), or a control substrate not previously occupied (Blank).

mothers in the *H. helluo* treatment on day one of the experiment. In our study we did not renew the silk and excreta over the six-day experimental period. Previous studies indicate that *P. milvina* response to *H. helluo* cues becomes reduced over time due to the age of the stimulus (Barnes et al. 2002) rather than habituation to the cues (Persons et al. 2002). Adult females have a strong response toward fresh silk and excreta deposited by an adult *H. helluo* less than 24 hours earlier but are less responsive to one week-old *H. helluo* cues (Barnes et al. 2002). Results observed here are consistent with Barnes et al. (2002) in that the effect of *H. helluo* cues appeared to have diminished over the duration of the experiment and may have contributed to the significant response during the first day but not on subsequent days.

Given the high activity level of *P. milvina* (Walker et al. 1999), we propose that even small differences in spiderling dismount frequencies across treatments may translate into favorable non-random site dispersal with respect to the presence of *H. helluo*. For now it remains unclear the extent to which variation in spiderling dismounts are attributable to spiderlings directly responding to predator cues or indirectly via subtle changes in the mother's behavior in the presence of these cues. However, spiderling dispersal via other mechanisms should be considered as well. The prevalence of aerial ballooning or other forms of secondary dispersal in *P. milvina*

is unknown, but has been observed in other species in the genus (Richter 1970) and may further allow spiderling avoidance of areas with higher predation risk.

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## SHORT COMMUNICATION

# DISTRIBUTION OF SPIDERS ON DIFFERENT TYPES OF INFLORESCENCES IN THE BRAZILIAN PANTANAL

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**ABSTRACT.** Reproductive stems add complexity to vegetation, thereby increasing the range and quality of microhabitats available for arthropods. In this study, we evaluated whether variation in inflorescence characteristics influenced spider distribution. We compared spider guild structure among inflorescences of three herbaceous plant species, *Melanthera latifolia*, *Conyza bonariensis* and *Eupatorium hecatanthum* (Asteraceae), and between inflorescences of *C. bonariensis* in two different phenological stages, flower buds and opened flowers. Total spider abundance was higher on *M. latifolia*, intermediate on *E. hecatanthum*, and lower on *C. bonariensis*. Ambush spiders were more abundant on *M. latifolia* than on the other plant species, while the abundance of hunting spiders did not differ among plant species. Also, spiders recorded on *M. latifolia* were larger than those on both *E. hecatanthum* and *C. bonariensis*. However, ambush spiders were smallest on *M. latifolia*, while hunting spiders on *E. hecatanthum* were larger than on the other plant species. The number of spiders on inflorescences with flower buds did not differ from those with opened flowers, but ambush spiders on inflorescences with opened flowers were larger than those on inflorescences with flower buds. Our results with different inflorescence types support the hypothesis that differences on microhabitat structure influence distribution of spiders.

**Keywords:** Flower-dwelling spiders, Asteraceae, habitat structure

Habitat structure can influence the abundance, diversity and size distribution of spiders (Scheidler 1990; Evans 1997), since it is related to prey abundance, availability of refuges from predators and favorable microclimate conditions (Gunnarsson 1996; Halaj et al. 1998). Some studies have shown that the added complexity provided by higher densities of leaves and second order branchlets can result in increased abundances and mean body sizes of some species of plant-dwelling spiders (Hatley & MacMahon 1980; Gunarsson 1990; Halaj et al. 2000).

Inflorescences attract large numbers of herbivorous and pollinating insects due to the availability of pollen, nectar and edible tissues. The abundance of potential prey on plant reproductive stems can influence the assemblage of spiders that visit inflorescences (e.g., Morse & Fritz 1982; Nentwig 1993). In addition, the presence of inflorescences add another dimension to plant architecture by changing microclimate conditions and availability of refuges from predators. Structural characteristics of inflorescences such as branch size, texture, number and size of leaves and flowers, and the arrangement of the biomass in space vary both among plant species and between inflorescences in distinct phenological stages (opened flowers vs. flower buds) within a plant species. However, few studies have considered the use of flowers by spiders, and patterns of spider distribution on inflorescences of different plant species and/or in distinct phenological stages within the same plant species, are still obscure. In this study, we evaluated differences in the abundance and size distribution of crab spiders and hunting spiders among inflorescences of three plant species, and between reproductive stems in different phenological stages within the same plant species.

This study was carried out in November 2000 at the Miranda–Abobral subregion of the Pantanal do Mato Grosso, Central Brazil (19°34′S:57°00′W). The study area consists of natural forest fragments and gallery forests. These fragments have variable sizes, and are surrounded by seasonally flooded fields. Spiders were sampled from three species of herbaceous plants (Asteraceae), common at the edge of gallery forests on the riverside of Rio Miranda. The plant species sampled differed in several inflorescence characteristics: *Melanthera latifolia* (Gardn.) has a 40cm long inflorescence, with few (7.33 ± 1.53, mean ± SD; $n$ = 10) yellow flowers, each one with a corolla diameter of 6.5 ± 0.87cm

Table 1.—Results of one-way ANOVAs and multiple comparisons tests comparing the number and body size of spiders (means ± standard errors) in different guilds (ambush or hunter) on inflorescences from three species of Asteraceae at the edge of a gallery forest. Similar letters connect means that did not differ (Tukey's HSD, $P > 0.05$).

| Spiders | *M. latifolia* | *C. bonariensis* | *E. hecatanthum* | *F* | *P* |
|---|---|---|---|---|---|
| Number of spiders per inflorescence branch | | | | | |
| Total spiders | 11.7 ± 1.1[a] | 4.7 ± 3.1[b] | 8.0 ± 1.7[a,b] | 8.073 | 0.020 |
| Ambushers | 9.3 ± 0.4[a] | 2.0 ± 0.7[b] | 4.3 ± 2.0[b] | 13.069 | 0.007 |
| Hunters | 1.3 ± 1.1 | 1.7 ± 1.5 | 3.7 ± 0.8 | 1.792 | 0.245 |
| Body size of spiders (mm) | | | | | |
| Total spiders | 1.26 ± 0.07[a] | 1.54 ± 0.15[a] | 3.31 ± 0.82[b] | 10.705 | 0.010 |
| Ambushers | 1.20 ± 0.07[a] | 1.62 ± 0.10[b] | 1.82 ± 0.12[b] | 12.771 | 0.007 |
| Hunters | 1.87 ± 0.13[a] | 1.87 ± 0.13[a] | 4.41 ± 0.58[b] | 21.081 | 0.008 |

($n$ = 10); *Conyza bonariensis* (L.) Cronq. has a 48cm long inflorescence, with many (33.0 ± 3.60; $n$ =10) white flowers (corolla diameter = 1.30 ± 0.10cm); *Eupatorium hecatanthum* (DC.) Bak.has an inflorescence 12cm long, purple flowers (corolla diameter = 3.47 ± 0.15cm) and an intermediate number of flowers per inflorescence (22.67 ± 2.52) compared to the other two species. All plant species occurred together within the patches in the sampling sites. They grew intertwined, so that spiders could move from one species to another without spatial barriers.

Samples were made at three distinct sites (replicates) in the edge of the gallery forest. At each site, we collected 10 mature inflorescences (with opened flowers) from each plant species along a 50m transect. The inflorescences were carefully put in a plastic bag and cut at the stem base. Once in the laboratory, the spiders from each stem were removed, identified to family level, and preserved in 70% ethanol. The spiders were categorized into functional groups based on similarities of foraging behavior. Ambush spiders included only members of the family Thomisidae, whereas hunting spiders included the families Salticidae, Oxyopidae, Clubionidae and Anyphaenidae. Web-building spiders and other categories accounted for only 8.2% of all individuals sampled; they were not analysed according to foraging mode due to small sample sizes, and thus were only included in the analysis of the total number of spiders. The body length between chelicerae and spinnerettes of each individual spider was measured to the nearest 0.1mm. The voucher specimens were deposited in the Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul (ZUFMS).

We compared spider abundance and body size distribution between inflorescences in two phenological stages by collecting stems of *Conyza bonariensis* from the same sampling sites. At each site, we collected 10 young inflorescences which had only flower buds, and 10 mature inflorescences with opened flowers. We focussed on *C. bonariensis* because individual plants of this species with both types of inflorescence were abundant within each sampling site. Sampling procedures were the same as described above.

We used one-way ANOVA to compare the abundance and mean size of spiders both among the three plant species, and between inflorescences in distinct phenological stages (opened flowers vs. flower buds). We used Tukey's HSD multiple comparisons test following ANOVA to determine differences among plant species. We considered that stems sampled within a site were pseudoreplicates, so the variance associated with them was discarded, resulting in three replicates for each treatment level (see Hurlbert 1984). Our significance level was 0.05. Data were transformed to $\log_{10}$ to obtain normality and homogeneity of variances.

**Influence of plant species on spider abundance and body size distribution.**—The total number of spiders on inflorescences differed among the three plant species. Spiders were more abundant on *M. latifolia* followed by *E. hecatanthum*, whereas *C. bonariensis* had the lowest number of spiders (Table 1). The distribution of ambush and hunting spiders differed among plant species. Ambush spiders were more common on *M. latifolia* compared to both *C. bonariensis* and *E. hecatanthum*, whereas the abundance of hunting spiders did not differ among plant species (Table 1).

Prey availability is regarded as one of the main factors that determine spider abundance (Morse & Fritz 1982; Greenstone 1984; Henschell & Lubin 1997). Although we did not estimate the number of potential prey attracted to the inflorescences of the three plant species, *Melanthera latifolia* is probably more visited by insects than both *C. bonariensis* and *E. hecatanthum*, because it has larger flowers. Inflorescences are regarded as an advertising unit, and several studies showed that larger and more

Table 2.—Results of one-way ANOVAs comparing total number of spiders and abundances of ambush and hunting spiders on inflorescences of *Conyza bonariensis* (Asteraceae) in distinct phenological stages (opened flowers vs flower buds).

| Spiders | Flower buds | Opened flowers | $F$ | $P$ |
|---|---|---|---|---|
| Total spiders | 7.3 ± 3.2 | 4.7 ± 3.1 | 1.085 | 0.356 |
| Ambushers | 4.0 ± 3.0 | 2.0 ± 1.0 | 0.781 | 0.427 |
| Hunters | 2.0 ± 1.7 | 1.7 ± 2.1 | 0.172 | 0.700 |

opened flowers attract more insects (e.g., Bell 1985; Cohen & Shmida 1993; Bernays and Chapman 1994; Dafni et al. 1997). Thus, *M latifolia* may be more attractive to spiders than the other species.

Mean body size of spiders sampled on inflorescences also differed among plant species. Spiders on *E. hecatanthum* were larger than those on *C. bonariensis* and *M. latifolia* (Table 1). Ambush spiders on *M. latifolia* were significantly smaller than those on *C. bonariensis* and *E. hecatanthum*. However, hunting spiders found on inflorescences of *E. hecatanthum* were larger than those on both *C. bonariensis* and *M. latifolia*, which sheltered similar sized spiders. Although larger insects may be more frequently attracted by large flowers (Dafni et al. 1997) and could potentially attract larger spiders (Nentwig 1993), studies on vegetative branches show that large spiders are more vulnerable to bird predation (Waldorf 1976; Askenmo et al. 1977). Other structural features of the plants such as branch structural complexity may influence the microhabitat choice by larger spiders due to differences in the availability of refuges against predators (Gunarsson 1990, 1996; Halaj et al. 2000). Thus, there is a need for more studies on the distribution of spiders in distinct inflorescence types, since spider groups may respond differently to traits of inflorescences from different plant species.

**Influence of phenological stage on spider abundance and size distribution.**—The total number of spiders on inflorescences of *C. bonariensis* with flower buds was not significantly different from those with opened flowers ($F_{1,4} = 1.085$; $P = 0.356$). The abundances of ambush and hunting spiders on both inflorescence types were also similar (Table 2). However, these results should be evaluated with caution. Among the plant species studied, the lowest abundance of spiders was recorded on *C. bonariensis*. The low number of spiders observed could obscure differences between inflorescences in distinct phenological stages, since inflorescences of this species were not very attractive for the spiders. Unfortunately, *C. bonariensis* was the only species in the study area with inflorescences in both phenological stages, and it was not possible to test this effect on plant species which sheltered larger numbers of spiders. On the other hand, spider body size differed between inflorescence types. Mean body size of ambush spiders was larger on inflorescences with opened flowers when compared with those bearing flower buds ($F_{1,4} = 17.826$; $P = 0.013$), but no differences in body size were recorded for hunting spiders ($F_{1,4} = 0.009$; $P = 0.930$). These data suggest that, at least for some spider groups, inflorescences in distinct phenological stages can represent differences in fine-grained qualities of the habitat such as hiding places or prey availability for larger spiders.

Several studies of plant-dwelling spiders on vegetative branches have shown a strong relationship between non-reproductive branch structure and distribution of different spider guilds (Hatley & MacMahon 1980; Scheidler 1990; Uetz et al. 1999; Halaj et al. 2000). Our results suggest that inflorescence structure and architecture also influences spider assemblages, since spiders were more abundant on some types of inflorescence than on others, and mainly because inflorescences of distinct plant species attracted spiders with different foraging strategies. Greco and Kevan (1994) demonstrated that even without any available prey, *Misumena vatia* (Clerck) was attracted to yellow color and to a specific plant species, and proposed that these spiders use vision to select microhabitats. In addition, Louda (1982) detected differences in the abundances of *Peucetia viridans* (Hentz) (Oxyopidae) on inflorescences of two *Haplopappus* species (Asteraceae), suggesting that either inflorescence morphology could influence prey availability, or inflorescence type could provide some unknown favorable characteristics for those spiders. Inflorescence dwelling spiders can represent an excellent system to clarify questions about which variables influence the distribution of this important arthropod group on the vegetation, because inflorescences have special microhabitat characteristics when compared to non-reproductive branches, potentially influencing the composition and abundance of spider prey and predators attracted to these patches.

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## SHORT COMMUNICATION

# ITS2 rDNA VARIATION OF TWO BLACK WIDOW SPECIES, *LATRODECTUS MACTANS* AND *LATRODECTUS HESPERUS* (ARANEAE, THERIDIIDAE)

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**ABSTRACT.** The taxonomic status of two closely related species of *Latrodectus*, *L. mactans* and *L. hesperus*, has been debated for many years. Based on morphological characteristics and genitalia, some workers consider them as valid species and others as subspecies. This study was conducted to determine whether the internal transcribed spacers 2 (ITS2) of rDNA exhibit sequence differences between the two taxa that could delineate their taxonomic relationship. Individuals of *L. mactans* and *L. hesperus* from six populations were collected and identified based on morphological characteristics. The ITS2 rDNA of nine individuals was sequenced and analyzed. Results indicate that the minimal differences present in the ITS2 sequences are taxonomically insignificant.

**Keywords:** Theridiidae, *Latrodectus*, rDNA, internal transcribed spacer 2

The literature reveals conflicting information concerning the taxonomic status of two black widow species, *Latrodectus mactans* (Fabricius 1775) and *L. hesperus* Chamberlin & Ivie 1935 (Araneae, Theridiidae). Taxonomic work based on morphological characteristics has produced controversial conclusions. The two spider taxa were designated as subspecies by Levi (1959), and as separate species by Kaston (1970, 1978). For this study, the spiders were identified to species following the characteristics outlined by Kaston. Specimens of each species are on deposit in the Invertebrate Collection at Midwestern State University, Wichita Falls, Texas.

The rRNA genes have long been recognized as attractive markers for phylogenetic studies (Hillis & Dixon 1991). These genes are organized in clusters of repeated units, each of which consists of coding sequences, and several transcribed and non-transcribed spacer regions (NTS). The transcription units include the 18S, 5.8S, and 28S genes as well as external and internal transcribed spacers (ETS and ITS). Coding regions and spacers differ greatly in their rate of evolution, and hence the rDNA clusters have the potential to reveal phylogenetic relationships at many taxonomic levels. The level of divergence observed in the spacer regions is appropriate for detecting differences between specific individuals, which provides a potentially useful marker with which to study the relationships of populations and closely related species (Cerbah & Souza 1998; Hedin 1997; Vogler 1994). For example, Vogler (1994) separated tiger beetles (*Cicindela dorsalis*); Hedin (1997) separated cave spider populations and species (*Nesticus*); Harris & Crandall (2000) separated closely related species and populations of freshwater crayfishes (Decapoda, Cambaridae).

This preliminary study of ITS2 rDNA variation was conducted using individuals from three populations for each species. *Latrodectus mactans* individuals were collected in Texas from Wichita (34°00′N, 98°42′W), Brown (31°45′N, 99°00′W) and Kimble (30°29′N, 99°46′W) Counties. *Latrodectus hesperus* individuals were collected from Eddy County, New Mexico (32°52′N, 104°45′W), Brewster (29°33′N, 103°47′W) and Garza (33°10′N, 101°20′W) Counties of Texas. Genomic DNA was isolated from leg IV of each individual spider using QIAGEN DNAeasy Tissue Kit (Qiagen, Inc., Valencia, CA). The DNA concentration was measured using a UV spectrophotometer (Pharmacia, Ultraspec III).

The ITS2 region of rDNA was amplified using 5.8S primer (5′-GGGACGATGAAGAACGCAGC-

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Lat CAGCTGCGAGACTTGGTGTGAATTGCAGGACACATTGAGCACTGATTTTTCGAACGCGCA
Eno CAGCTGCGAGACT-GGTGTGAATTGCAGGACACATTGAGCACTGATTTTTCGAACGCGCA
    ************ ********************************************

Lat TTGCGCCCTCT-----TCCCCGGGGGCTCGCCTGTCTGAGGGTCGGATAAGACTTACCGA
Eno TTGCGGCCTCGGGTCCTGCCCGGGGCCTCGCCTGTCTGAGGGTCGGATAAGACTTGCAAA
    ***** ****       * ******* ***************************** *  *

Lat GGAGGGTTTCCCTCCCA-TTGGCTGCATCGGATGG---TGATCATCCGTCTGCCTAAGGT
Eno GGAAAGTTCGCTTTCCACTTGGCCGAACCGGATCGCTTTTGTGGTTCGCCGGCTTAAGGT
    ***  ***  * * *** ***** * * ***** *   *      * ** * ** ******

Lat CTTCGTCCGCGAATCCCCCTGGCCGAGAAGCGTCGCTCC---TCGAATAGGTCCAGCATA
Eno TTACG-----GATCCTCCCCGGCCGAGAAGCGTGGCTCCCACTTGACCAACGCTCGCGG-
     * **      **  * *** ************ *****   * **  *   *  **

Lat GAGGGAGAACGACTGA-TCGTCTCCCCGCCGACTGGAGCTGGAGCTGATGACGCAGAGAG
Eno GCTGGAGAA-GACTGAGTAGTTTCTCCGCTGAAGCGAGCGACGGGAGCGAGCGCAGAGAG
    *  ****** ****** * ** ** **** **   ****    *  *    *********

Lat TGTGCCGGGAAGAAGGGATGGTCGGATGGTCCGCTTGGGTGCTTTCGTGCTAATGCGTCC
Eno CTTGCCGAGGAGA-----------GATCCTCCAC--------------------GCGTGC
      ***** * ***           ***  *** *                    **** *

Lat CTCGTTCGTATAACGGCGTTGAACTACGTCCTGAATTGAGGGTTCGCAGCGAAAGGTCAC
Eno C-----------AC-----------------------------TGGCACGGTAAACTCAA
    *           **                             * ***  * **  ***

Lat GACTGATATTCATATCTGTCGACCTCAGATCAGACGAGATGACCCGCTGAATTTAA
Eno AA---------ATAT-TGTCGACCTCAGATCAGACGAGATGACCCGCTGAATTTAA
     *         **** ****************************************
```

Figure 1.—Alignment of ITS2 regions from *Latrodectus* spp. and *Enoplognatha ovata*. Lat. = consensus sequence of eight *Latrodectus mactans* and *Latrodectus hesperus* individuals. Eno. = sequence of *E. ovata* (Araneae, Theridiidae). Underlined ITS2 sequences are flanked by 5.8S and 28S sequences. Asterisks indicate identical nucleotide positions. Alignment generated by CLUSTALW 1.4.

3′) and 28S primer (5′-TCCTCCGCTTATTGATATGC-3′) (Hillis et al. 1996). Two nanograms of spider genomic DNA were used for each reaction and PCR amplification was performed in 100 μL, using the following profile: 5 min at 94 °C, 40 cycles (1 min at 94 °C, 2 min at 45 °C, 1.5 min at 72 °C), and 7 min at 72 °C. The products were assessed by mini-gel electrophoresis using 5 μL aliquots. Successful amplifications generated a single 0.5 kb product. After purification, the PCR products were digested with *Eco*R I and *Hin*d III and ligated into pUC19 vector. The recombinant plasmids were transformed into *E. coli* DH5α cells. Sequences of both strands were determined by Northwoods DNA, Inc. (Center for Research and Innovation, 44526 CNTY Rd 3, Becida, MN 56678). Results were received as unprocessed nucleotide sequences and analyzed manually. Some visual adjustments were made. The individual sequences were aligned using CLUSTAL W 1.4 (Higgins & Sharp 1988) and consensus sequences were obtained.

First, the extent of the intergenic region between the 5.8S and 28S coding regions referred to as ITS2 was determined by similarity with the published sequences of *Enoplognatha ovata* (Araneae; Theridiidae) (Fig. 1) (Tan & Gillespie 1999). The length of the ITS2 region in different clones of *L. mactans* and *L. hesperus* is ~360 bp. Three individuals (LMW1, LMW2, LMW3) of the LMW population (*L. mactans* from Wichita County, Texas) were selected to analyze the variation in one population. For individual LMW3, four separate clones were sequenced to test variation within one individual. For the other populations, one individual from each was randomly selected for PCR amplification and one or more independent clones covering the ITS2 were sequenced from each of these individuals.

Five variable nucleotide positions were found in

| | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| LMW1 | C | T | T | T |
| LMW2 | C | T | T | C |
| LMJ | T | T | A | T |
| LMB | T | A | T | T |
| LHM | T | A | T | T |
| LMW3 | T | T | A | T |
| LHD | T | T | T | T |
| LHX | T | T | A | T |

Figure 2.—Alignment of Variable ITS2 sites from eight *Latrodectus* individuals. Variable nucleotides occur at four positions within the *Latrodectus* consensus sequences in Figure 1: 1 = 124; 2 = 153; 3 = 227; 4 = 422. LMW = *L. mactans*, Wichita County, Texas; LMJ = *L. mactans*, Llano County, Texas; LMB = *L. mactans*, Brown County, Texas; LHM = *L. hesperus*, Eddy County, New Mexico; LHD = *L. hesperus*, Brewster County, Texas; LHX = *L. hesperus*, Garza County, Texas.

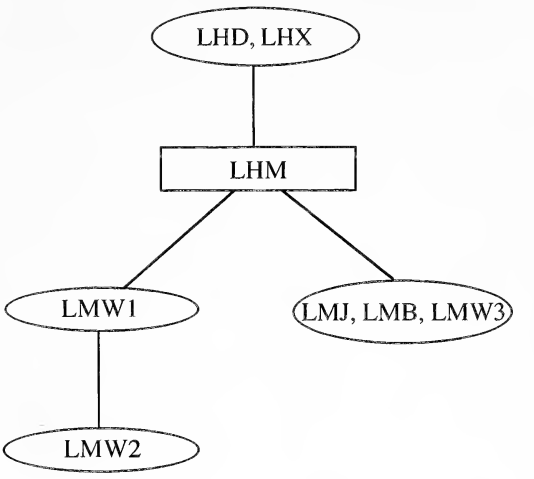


Figure 3.—Phylogenetic network of five haplotypes from ITS2 sequences of eight *Latrodectus* individuals. Open shapes, representing the haplotypes, indicate the included *Latrodectus* individuals. Analysis was performed by TCS (Clements et al. 2001).

the alignment of sequences from individual LMW3. Three variable nucleotide positions were found in the alignment of three individuals from Wichita County population of *L. mactans*. Three variable nucleotide positions were found in the alignment of three *L. mactans* populations. Only one variable nucleotide position was found among three populations of *L. hesperus*. The consensus sequences of eight individuals from six populations varied at four nucleotide positions (Fig. 2).

The phylogenetic analysis of the aligned sequences was performed as described by Templeton et al. (1992) using the TCS software package (Clement et al. 2000). ITS2 sequences from eight *Latrodectus* individuals collapsed into five haplotypes (Fig. 3). The three LMW individuals represented three different haplotypes on two different branches from a *L. hesperus* node. LMW3 and two *L. mactans* individuals from outside Wichita County represented a single haplotype. *Latrodectus hesperus* sequences collapsed into two haplotypes, one of which supported the two *L. mactans* branches.

Even though all the clones, individuals, populations and two taxa showed some level of sequence variation in the ITS2 region of rDNA, the separation between species was not well supported on these grounds. For *L. mactans*, variation within an individual is 1.4%, variation among individuals and that among populations are each 0.83%. The *L. hesperus* populations exhibit only 0.27% variation. The variation between two taxa is 0.83% and does not distinguish these two species. The same result was found in the ITS2 research of mosquitoes. Wesson et al. (1992) reported 0.46% variation within 10 clones of ITS2 from a single mosquito, *Aedes simpsoni*, while intraspecific variation in *A. aegypti* was only 1.17%. The differentiation even within a single individual may be caused by the existence of polymorphisms among repeat units of rDNA.

In a phylogenetic analysis of ITS2 sequence variations, *L. mactans* individuals from Wichita County represented as many haplotypes as the other five individuals, which included representatives of both *L. hesperus* and *L. mactans*. Furthermore, the three LMW haplotypes represented two distinct branches from LHM. Assuming that the Wichita County *L. mactans* individuals reflect a typical level of regional variation, ITS2 sequences do not offer a reliable means of distinguishing between *L. mactans* and *L. hesperus* populations.

Only those characters that are diagnostic for all individuals of an entire population can be used in the phylogenetic reconstruction of populations (Vogler 1994). Further exploration of the molecular taxonomy of these taxa will require additional data, including sequence comparisons of mtDNA, ITS1 DNA, plus other nuclear genes.

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Figures 1-4.— *A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

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